JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME XVI. OCTOBER, 1935 NUMBER 4

THE HOSTS, LIFE HISTORY AND CONTROL OF GYMNOSPORANGIUM CLAVIPES C. AND P.

IVAN H. CROWELL

With plates 155–160

TABLE OF CONTENTS

I. INTRODUCTION

GYMNOSPORANGIUM CLAVIPES C. and P., commonly referred to as the quince rust fungus, was one of the earliest species of the genus to be defined in North America. Schweinitz (1832) described it from the aecial phase occurring on *Crataegus* sp. as *Caeoma (Peridermium) germinale*. Later, Cooke and Peck (1871) described the telial phase of a rust on *Juniperus virginiana* L. as *Podisoma (Gymnosporangium) clavipes*. It was not until 1886, however, that Thaxter (1887) demonstrated by means of controlled cultures that these were but two phases of the same organism. Throughout the literature both specific names have been used. Some authors have followed Kern (1911) in calling the species *G. germinale* (Schw.) Kern. But Sydow (1915), Arthur (1934) and other mycologists adhere to the International Rules of Nomenclature and so designate the species *G. clavipes* C. & P.

The prevalence and destructiveness of the diseases caused by *G. clavipes* on ornamental pomaceous hosts and on many orchard varieties of apples, as well as on red cedars, have occasioned numerous inquiries regarding the pathogenicity and control of this rust. The information pertainable to these matters has been so meagre that comprehensive studies on the causal organism and the diseases produced by it were begun four years ago. The results obtained are presented in this paper. Certain phases of the investigations not yet completed are being continued.

The main lines of my investigations are as follows:

1. A determination by means of cultures and field observations of the pomaceous hosts of *G. clavipes* together with a discussion of their taxonomic position and geographic range.

2. Similar determinations and discussions of the Juniperus hosts of *G. clavipes*.

3. The symptomatology of the diseases caused by *G. clavipes*.

4. A thorough examination of the life history of *G. clavipes* on pomaceous and Juniperus hosts.

5. The practicability of fungicidal and of eradicative control measures of the diseases caused by *G. clavipes*.

II. THE POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P., THEIR TAXONOMIC POSITIONS AND THEIR GEOGRAPHIC RANGE

Contributions to our knowledge of the pomaceous hosts of *G. clavipes* as determined by artificial cultures are due chiefly to the work of Thaxter (1887), Arthur (1910, 1912), Thomas and Mills (1929) and Miller (1932). Numerous other investigators, by their field observations, have added several species to the list of pomaceous hosts. The total number previously reported is about thirty-six species in seven genera distributed as follows: *Amelanchier* (8), *Aronia* (3), *Chaenomeles* (1), *Crataegus* (20), *Cydonia* (1), *Malus* (2), *Pyrus* (1).

In my own studies on the pomaceous hosts, 701 species and varieties in 15 genera were inoculated, following essentially the same procedure described in a previous article (1934). These genera and the number of species of each inoculated are — *Amelanchier* (18), *Amelosorbus* (1), *Aronia* (4), *Chaenomeles* (2), *Crataegomespilus* (1), *Crataegus* (588), *Cydonia* (1), *Malus* (44), *Photinia* (1), *Pyrus* (19), *Sorbaronia* (1), *Sorbopyrus* (1), *and Sorbus* (17). One species of *Comptonia* and two of *Myrica* were also inoculated. From the results obtained the inoculated plants were placed in two groups. Those plants which developed no evidence of infection were classed as immune; while those plants on which infection was evident were classed as susceptible. The number of hosts determined by artificial inoculations was augmented by field observations in the Arnold Arboretum, on private estates about Boston and from the reports of former investigators.

The results showed that more than 480 species and varieties of pomaceous plants (including 48 varieties of orchard apples) scattered among eleven genera are susceptible. These hosts are presented in table 1.

TABLE I. POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P.[1]

Amelanchier alnifolia Nutt., *A. Bartramiana* Roem. (*A. oligocarpa* [Michx.] Roem.), *A. Bartramiana* × *laevis, A. Bartramiana* × *oblongifolia, A. canadensis* Med., *A. canadensis nana, A. erecta* Blanch., *A. florida* Lindl., *A. intermedia* Spach., *A. laevis* Wieg., *A. laevis* × *humilis, A. oblongifolia* (Torr. and Gray) Roem., *A. sanguinea* DC., *A. spicata* K. Koch, *A. stolonifera* Wieg.

Amelosorbus Jackii Rehd.

[1]For the taxonomy of the genus *Crataegus,* Palmer (1925) was used. Mr. Palmer has kindly checked the hosts of *G. clavipes* in the genus *Crataegus* against his revised but unpublished catalogue of *Crataegi.* For the taxonomy of the other genera, Rehder's Manual (1927) was followed as far as possible.

Aronia arbutifolia (L.) Ell., *A. floribunda* Spach (*A. arbutifolia atropurpurea* [Britt.] B. L. Robinson), *A. melanocarpa* Ell., *A. melanocarpa elata* Rehder, *A. monstrosa* Zabel.

Chaenomeles japonica Lindl., *C. lagenaria* Koidz., *C. lagenaria marmorata, C. lagenaria foliis rubris, C. lagenaria sanguinea semiplena.*

Crataegomespilus grandiflora Bean.

Crataegus

ANOMALAE: *C. affinis* Sarg., *C. asperifolia* Sarg., *C. Brockwayae* Sarg., *C. Coleae* Sarg., *C. cyclophylla* Sarg., *C. Dunbari* Sarg., *C. Egglestonii* Sarg., *C. e. ata* Sarg., *C. honesta* Sarg., *C. Ideae* Sarg., *C. improvisa* Sarg., *C. misella* Sarg., *C. pinguis* Sarg., *C. putata* Sarg., *C. repulsans* Sarg., *C. Saundersiana* Sarg., *C. scabrida* Sarg., *C. shirleyensis* Sarg., *C. urbana* Sarg.

COCCINEAE: *C. acclivis* Sarg., *C. arcuata* Ashe, *C. assurgens* Sarg., *C. aulica* Sarg., *C. caesa* Ashe, *C. chippewaensis* Sarg., *C. confinis* Sarg., *C. conspecta* Sarg., *C. cristata* Ashe, *C. delecta* Sarg., *C. densiflora* Sarg., *C. elongata* Sarg., *C. fluviatilis* Sarg., *C. fretalis* Sarg., *C. Hillii* Sarg., *C. Holmesiana* Ashe, *C. Holmesiana tardipes* Sarg., *C. lenta* Ashe, *C. Macounii* Sarg., *C. miranda* Sarg., *C. neolondinensis* Sarg., *C. pedicellata* Sarg., *C. perrara* Sarg., *C. polita* Sarg., *C. Pringlei* Sarg., *C. pura* Sarg., *C. sejuncta* Sarg., *C. sertata* Sarg., *C. Thayeri* Sarg., *C. vivida* Sarg.

CRUS-GALLI: *C. arborea* Beadle, *C. arduennae* Sarg., *C. armata* Sarg., *C. attenuata* Sarg., *C. barrettiana* Sarg., *C. Bartramiana* Sarg., *C. bellica* Sarg., *C. calophylla* Sarg., *C. Canbyi* Sarg., *C. cerasina* Sarg., *C. crus-galli* L., *C. crus-galli arbutifolia* Hort. ex Nicholson, *C. crus-galli exigua* Sarg., *C. crus-galli pyracanthifolia* Ait., *C. crus-galli rubens* Sarg., *C. crus-galli splendens* Ait., *C. effulgens* Sarg., *C. erecta* Sarg., *C. Farwellii* Sarg., *C. Fontanesiana* (Spach) Steudel, *C. geneseensis* Sarg., *C. insignis* Sarg., *C. Lavallei* Herincq, *C. lawrencensis* Sarg., *C. leptophylla* Sarg., *C. livoniana* Sarg., *C. macra* Beadle, *C. pachyphylla* Sarg., *C. Palmeri* Sarg., *C. parciflora* Sarg., *C. Pennypackeri* Sarg., *C. peoriensis* Sarg., *C. persimilis* Sarg., *C. phlebodia* Sarg., *C. Reverchonii* Sarg., *C. rivalis* Sarg., *C. robusta* Sarg., *C. rubrifolia* Sarg., *C. rudis* Sarg., *C. triumphalis* Sarg.

DILATATAE: *C. coccinoides* Ashe, *C. dilatata* Sarg.

DOUGLASIANAE: *C. colorado* Ashe, *C. columbiana* Howell, *C. Douglasii* Lindl., *C. Douglasii* f. *badia* Sarg., *C. Douglasii Suksdorfii* Sarg., *C. erythropoda* Ashe, *C. Piperi* Britt., *C. rivularis* Nutt. apud Torr. & Gray.

FLAVAE: *C. colonica* Beadle, *C. dispar* Beadle, *C. flava* Ait., *C. ignava* Beadle.

INTRICATAE: *C. Delosii* Sarg., *C. flavida* Sarg., *C. modesta* Sarg., *C. nemoralis* Sarg., *C. neobushii* Sarg., *C. scabra* Sarg., *C. straminea* Beadle.

MACRACANTHAE: *C. admiranda* Sarg., *C. aquilonaris* Sarg., *C. ardua* Sarg., *C. baccata* Sarg., *C. Beckiana* Sarg., *C. bristolensis* Sarg., *C. calpodendron* (Ehrh.) Med., *C. Calvinii* Sarg., *C. chadfordiana* Sarg., *C. corporea* Sarg., *C. Deweyana* Sarg., *C. divida* Sarg., *C. Emersoniana* Sarg., *C. ferentaria* Sarg., *C. ferta* Sarg., *C. fertilis* Sarg., *C. finitima* Sarg., *C. flagrans* Sarg., *C. fulgens* Sarg., *C. gemmosa* Sarg., *C. glabrata* Sarg., *C. Handyae* Sarg., *C. hystricina* Ashe, *C. laxiflora* Sarg., *C. macracantha* Lodd., *C. membranacea* Sarg., *C. microsperma* Sarg., *C. missouriensis* Ashe, *C. neofluvialis* Ashe, *C. occidentalis* Britt., *C. ogdenburgensis* Sarg., *C. peramoena* Sarg., *C. prunifolia* (Marsh.) Pers., *C. radiosa* Sarg., *C. rhombifolia* Sarg., *C. Robinsonii* Sarg., *C. Searsii* Sarg., *C. spatiosa* Sarg., *C. spinulosa* Sarg., *C. structilis* Ashe, *C. succulenta* Schrader, *C. tomentosa* L., *C. truculenta* Sarg., *C. vegeta* Sarg.

MICROCARPAE: *C. Phaenopyrum* (L. f.) Med., *C. spathulata* Michx.

MOLLES: *C. anomala* Sarg., *C. arnoldiana* Sarg., *C. champlainensis* Sarg., *C. contortifolia* Sarg., *C. digna* Sarg., *C. dispessa* Ashe, *C. Ellwangeriana* Sarg., *C. exclusa* Sarg., *C. Fulleriana* Sarg., *C. induta* Sarg., *C. invisa* Sarg., *C. lanuginosa* Sarg., *C. lasiantha* Sarg., *C. lauta* Sarg., *C. limaria* Sarg., *C. mollis* (Torr. & Gray) Scheele, *C. nutans* Sarg., *C. pennsylvanica* Ashe, *C. peregrina* Sarg., *C. Robesoniana* Sarg., *C. sera* Sarg., *C. submollis* Sarg.; *C. Tatnalliana* Sarg., *C. urbica* Sarg.

OXYACANTHAE: *C. altaica* Lange, *C. hiemalis* Lange, *C. Heldreichii* Boiss., *C. intermedia, C. Maximowiczii* Schneider, *C. monogyna* Jacq., *C. monogyna albo-plena* Schneider, *C. monogyna inermis* Rehd., *C. monogyna laciniata* Loud., *C. monogyna pteridifolia* Rehd., *C. monogyna spectabilis, C. monogyna stricta* Loud., *C. monogyna versicolor, C. Oxyacantha* L., *C. Oxyacantha Gireoudi* Bean, *C. Oxyacantha alba* West., *C. Oxyacantha rubra* Schneider, *C. pinnatifida* Bunge, *C. sorbifolia* Lange, *C. Wilsonii* Sarg.

PRUINOSAE: *C. arcana* Beadle, *C. aridula* Sarg., *C. aspera* Sarg., *C. austera* Sarg., *C. beata* Sarg., *C. bellula* Sarg., *C. brachypoda* Sarg., *C. bracteata* Sarg., *C. cestrica* Sarg., *C. cognata* Sarg., *C. comparata* Sarg., *C. confragosa* Sarg., *C. delawarensis* Sarg., *C. disjuncta* Sarg., *C. dissona* Sarg., *C. divisifolia* Sarg., *C. Ferrissii* Ashe, *C. formosa* Sarg.,

C. fusca Sarg., *C. georgiana* Sarg., *C. glareosa* Ashe, *C. horridula* Sarg., *C. incisa* Sarg., *C. Jesupii* Sarg., *C. Kellermanii* Sarg., *C. latifrons* Sarg., *C. levis* Sarg., *C. macrocalyx* Sarg., *C. numerosa* Sarg., *C. patrum* Sarg., *C. pequotorum* Sarg., *C. perampla* Sarg., *C. perjucunda* Sarg., *C. philadelphica* Sarg., *C. platycarpa* Sarg., *C. pruinosa* (Wendl.) K. Koch, *C. pulchra* Sarg., *C. relicta* Sarg., *C. remota* Sarg., *C. rubicundula* Sarg., *C. sicca* Sarg., *C. tribulosa* Sarg.

PRUNIFOLIAE: *C. decorata* Sarg.

PUNCTATAE: *C. amnicola* Beadle, *C. angustata* Sarg., *C. barbara* Sarg., *C. Brownietta* Sarg., *C. calvescens* Sarg., *C. celsa* Sarg., *C. compacta* Sarg., *C. desueta* Sarg., *C. florifera* Sarg., *C. glabrifolia* Sarg., *C. incaedua* Sarg., *C. Lettermanii* Sarg., *C. notabilis* Sarg., *C. pausiaca* Ashe, *C. porrecta* Ashe, *C. praestans* Sarg., *C. pratensis* Sarg., *C. punctata* Jacq., *C. punctata aurea* Ait., *C. punctata canescens* Britt., *C. rigens* Beadle, *C. suborbiculata* Sarg., *C. succincta* Sarg., *C. tenax* Ashe, *C. verruculosa* Sarg.

ROTUNDIFOLIAE: *C. Bicknellii* Eggl., *C. Blanchardii* Sarg., *C. Brainerdii* Sarg., *C. Brunetiana* Sarg., *C. chrysocarpa* Ashe, *C. coccinata* Sarg., *C. cupilifera* Sarg., *C. Dodgei* Ashe, *C. inaudita* Sarg., *C. Jonesae* Sarg., *C. Kennedyi* Sarg., *C. kingstonensis* Sarg., *C. maligna* Sarg., *C. Margaretta* Ashe, *C. Margaretta xanthocarpa* Sarg., *C. Maribella* Sarg., *C. Oakesiana* Eggl., *C. praecoqua* Sarg., *C. Proctoriana* Sarg., *C. propria* Sarg., *C. rotundata* Sarg., *C. rotundifolia* Moench, *C. rotundifolia pubera* Sarg., *C. rotundifolia* f. *rubescens* Sarg., *C. varians* Sarg., *C. Websteri* Sarg.

SILVICOLAE: *C. allecta* Sarg., *C. Barryana* Sarg., *C. blairensis* Sarg., *C. compta* Sarg., *C. delectata* Sarg., *C. diffusa* Sarg., *C. dissona* Sarg., *C. effera* Sarg., *C. filipes* Ashe, *C. foliata* Sarg., *C. Fretzii* Sarg., *C. iracunda* Beadle, *C. iterata* Sarg., *C. Livingstoniana* Sarg., *C. luxuriosa* Sarg., *C. medioxima* Sarg., *C. opulens* Sarg., *C. promissa* Sarg., *C. prona* Ashe, *C. radina* Sarg., *C. recordabilis* Sarg., *C. ruricola* Sarg., *C. stolonifera* Sarg., *C. strigosa* Sarg., *C. tortuosa* Sarg., *C. xanthocarpa* Sarg.

TENUIFOLIAE: *C. acuminata* Sarg., *C. acutiloba* Sarg., *C. alnorum* Sarg., *C. apiomorpha* Sarg., *C. ascendens* Sarg., *C. asperata* Sarg., *C. bella* Sarg., *C. benigna* Sarg., *C. blandita* Sarg., *C. Boothiana* Sarg., *C. colorata* Sarg., *C. conferta* Sarg., *C. crudelis* Sarg., *C. cyanophylla* Sarg., *C. Damei* Sarg., *C. delucida* Sarg., *C. demissa* Sarg., *C. Edsoni* Sarg., *C. Eganii* Ashe, *C. firma* Sarg., *C. flabellata* (Bosc.) K. Koch,

C. florea Sarg., *C. Forbesae* Sarg., *C. fucosa* Sarg., *C. genialis* Sarg., *C. glaucophylla* Sarg.. *C. gracilipes* Sarg., *C. Gruberi* Ashe, *C. Habereri* Sarg., *C. Hadleyana* Sarg., *C. heidelburgensis* Sarg., *C. insolita* Sarg., *C. leptopoda* Sarg., *C. lucorum* Sarg., *C. luminosa* Sarg., *C. macrosperma* Ashe, *C. marcida* Ashe, *C. matura* Sarg., *C. media* Sarg., *C. merita* Sarg., *C. miniata* Ashe, *C. modica* Sarg., *C. monstrata* Sarg., *C. Napaea* Sarg., *C. nescia* Sarg., *C. otiosa* Ashe, *C. Paddockeae* Sarg., *C. Paineana* Sarg., *C. pallidula* Sarg., *C. parviflora* Sarg., *C. pastorum* Sarg., *C. paucispina* Sarg., *C. pentandra* Sarg., *C. perlevis* Ashe, *C. populnea* Ashe, *C. pumila* Sarg., *C. retrusa* Ashe, *C. roanensis* Ashe, *C. rubicunda* Sarg., *C. rubrocarnea* Sarg., *C. rufipes* Ashe, *C. sarniensis* Sarg., *C. serena* Sarg., *C. sextilis* Sarg., *C. Slavini* Sarg., *C. Streeterae* Sarg., *C. suavis* Sarg., *C. taetrica* Sarg., *C. tarda* Sarg., *C. tenella* Sarg., *C. tenera* Sarg., *C. tenuiloba* Sarg., *C. trachyphylla* Sarg., *C. viridimontana* Sarg., *C. vittata* Ashe.

TRIFLORAE: *C. conjungens* Sarg.

UNIFLORAE: *C. uniflora* Moench.

VIRIDES: *C. abbreviata* Sarg., *C. blanda* Sarg., *C. penita* Beadle, *C. velutina* Sarg., *C. viridis* L., *C. vulsa* Beadle.

Cydonia oblonga Mill.

Malus angustifolia Michx., *M. floribunda* Sieb., *M. ioensis plena* Rehd., *M. pumila* Mill., *M. spectabilis* Borkh., *M. sylvestris* Mill.

Photinia villosa DC.

Pyrus communis L., *P. sinensis* Lindl.

Sorbus americana Marsh, *S. dumosa* Greene.

A complete enumeration of all species and varieties of inoculated plants on which the results were negative is as follows:

Amelanchier amabilis Wieg., *A. asiatica* Endl., *A. grandiflora* Rehd., *A. humilis* Wieg., *A. humilis* × *sanguinea, A. ovalis* Med., *A. sera* Ashe.

Malus arnoldiana Sarg., *M. asiatica* Nakai, *M. atrosanguinea* Schneid., *M. baccata* Borkh., *M. baccata costata* Hort., *M. baccata gracilis* Rehd., *M. baccata Jackii* Rehd., *M. baccata mandshurica* Schneid., *M. baccata microcarpa* Regel., *M. baccata pendula* Hort., *M. brevipes* Rehd., *M. flexilis* Hort., *M. florentina* Schneid., *M. Halliana Parkmanii* Rehd., *M. Halliana spontanea* Rehd., *M. Hartwigii* Koehne, *M. honanensis* Rehd., *M. hupehensis* Rehd., *M. kansuensis* Schneid., *M.* spec. (*Pyrus Malus laurifolia* Gibbs), *M.* spec. (*Pyrus Lemoinei* Hort.), *M. magdeburgensis* Schoch, *M. micromalus* Mak., *M. orthocarpa* Lavall., *M. Prattii* Schneid., *M. pumila Niedzwetzkyana* Schneid., *M. purpurea* Rehd., *M. purpurea aldenhamensis* Rehd., *M. purpurea Eleyi* Rehd.,

M. robusta persicifolia Rehd., *M. Sargenti* Rehd., *M. Scheideckeri* Zabel, *M. Scheideckeri "Excellenz Thiel," M. sikkimensis* Koehne, *M. spectabilis Riversii* Nash, *M. sublobata* Rehd., *M. toringoides* Hughes, *M. trilobata* Schneid., *M. Tschonoskii* Schneid., *M. yunnanensis* Schneid., *M. yunnanensis Veitchii* Rehd., *M. zumi* Rehd., *M. zumi calocarpa* Rehd.

Pyrus amygdaliformis Vill., *P. Balansae* Decne., *P. betulifolia* Bge., *P. Bretschneideri* Rehd., *P. denticulata* Hort. Angl. ex Dum.-Cours., *P. elaeagrifolia* Pall., *P. Korshinskyi* Litv., *P. Lindleyi* Rehd., *P. longipes* Coss. & Dur., *P. Michauxii* Bosc., *P. nivalis* Jacq., *P. pashia* Buch.-Ham., *P. phaeocarpa* Rehd., *P. salvifolia* DC., *P. serotina* Rehd., *P. serrulata* Rehd., *P. syriaca* Boiss., *P. ussuriensis* Maxim.

Sorbaronia alpina superaria, S. spec.

Sorbopyrus auricularis bulbiformis Schneid.

Sorbus Aria Crantz, *S. arnoldiana* Rehd., *S. Aucuparia* L., *S. commixta* Hedl., *S. discolor* Hedl., *S. hybrida* L., *S. intermedia* Pers., *S. japonica calocarpa* Rehd., *S. Matsumurana* Koehne, *S. Meinichii* Hedl., *S. pohuashanensis* Hedl., *S. rotundifolia* Hedl., *S. subpinnata* Hedl., *S. thuringiaca* Fritsch (*S. decurrens* Hedl.).

Other plants inoculated were *Comptonia asplenifolia* Ait., *Myrica carolinensis* Mill. and *M. Gale* L.

In addition to the pomaceous hosts just reported, several varieties of orchard apples have been found by former investigators to be susceptible. A compilation of these is presented in table 2. Mills (1929) gives the following account of the occurrence of *G. clavipes* on orchard apples in New York: "Counts in 14 orchards in 4 counties showed fruit infection on Delicious (3 counts) 60 per cent; Fameuse (1 count) 21 per cent; Hubbardston (1 count) 28 per cent; McIntosh (15 counts) 18 per cent average; Winesap (2 counts) 74 per cent; Yellow Transparent (1 count) 84 per cent. Specimens were from 6 or 7 counties. Not found on foliage or twigs." This account and the fact that many other varieties of orchard apples are susceptible serve to stress the economic importance of *G. clavipes* to orchardists. In several orchards visited in Massachusetts the disease caused by *G. clavipes* was found to be particularly abundant on the Delicious variety. As high as 90 per cent of the fruits were attacked. This disease, one of the most severe on the Delicious apple, is of much concern to orchardists because this variety is being grown in greater quantities to meet the steadily increasing demands for it on the market.

TABLE II. THE RELATIVE SUSCEPTIBILITY OF ORCHARD APPLES TO G. CLAVIPES

Variety	Susceptible	Immune
Alexander	N. Y.	
Baldwin	Ind., Me., N. Y., N. S.	
Bechtel's Crab	Mass.	
Bellflower	Me.	
Ben Davis	N. Y.	Ind.
Bishop	N. S.	
Black Twig	Va., W. Va.	
Cortland	Me., N. Y.	
Crimson Beauty	N. S.	
Delicious	Ind., Me., Mass., N. Y., Tenn., Va., W. Va.	
Duchess	Me., N. Y.	
Early Red McIntosh	Me.	
Fameuse	N. Y., N. S.	
Family	N. S.	
Gideon	Ind.	
Golden Delicious	Me.	
Gravenstein	Me., N. Y., N. S.	
Grimes	Ind., Tenn.	
Hubbardston	N. Y.	
Jonathan	Ind., Me., N. Y.	Tenn.
King David	Ind.	
Maiden Blush	——	Ind.
McIntosh	Me., N. Y., N. S.	
Northern Spy	N. Y.	
Northwestern Greening	Ind., N. Y.	
Red Delicious	Me., N. Y., Tenn.	
Red Winesap	Tenn.	
R. I. Greening	N. Y., N. S.	
Ribston	N. S.	
Rome	Md., N. Y., Tenn., Vt., Va.	Ind.
Roxbury	N. S.	
Russett	N. Y., N. S.	
Stark	N. S.	
Starkey	Me., N. S.	
Starking	Me.	
Stayman	Ind., N. Y., Tenn., Va., W. Va.	

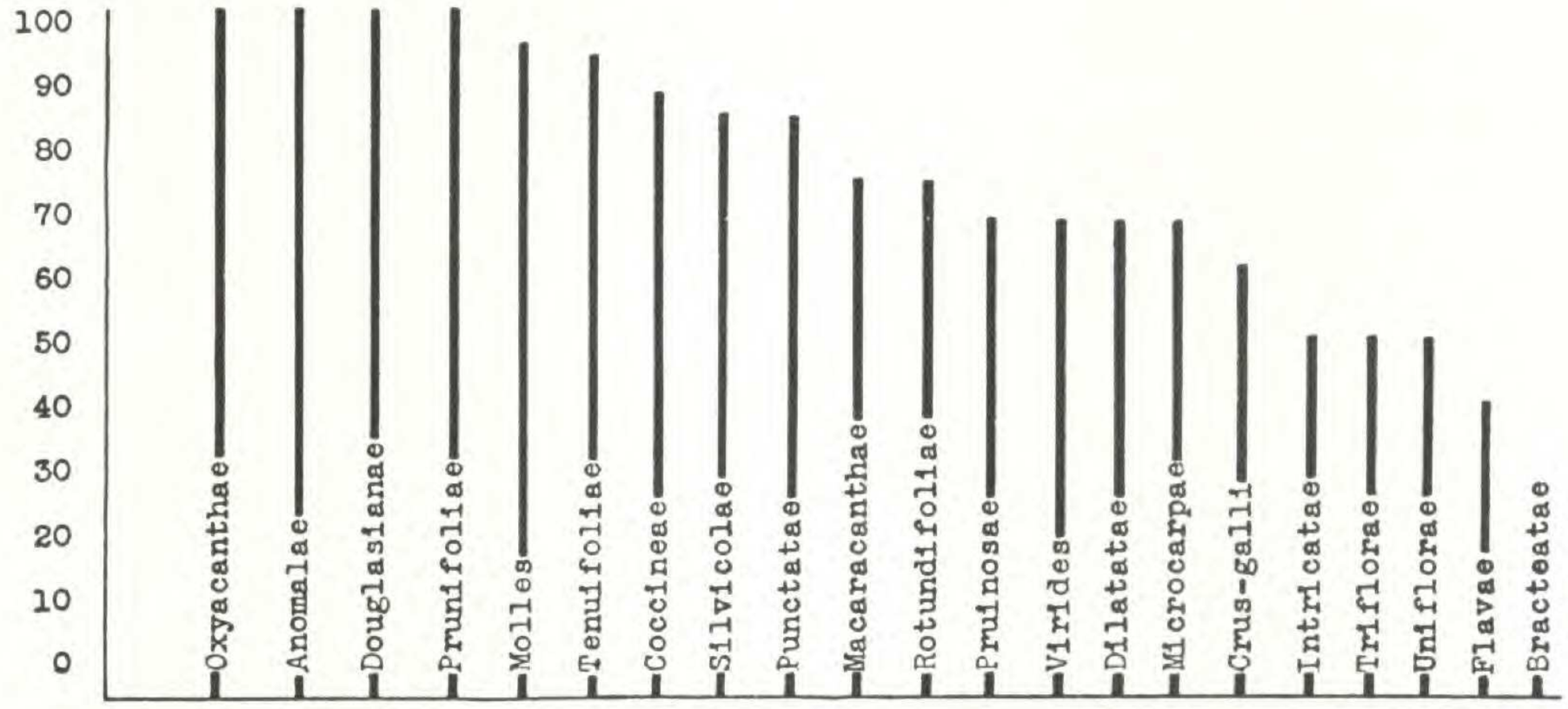
TABLE II. (*Continued*)

Variety	Susceptible	Immune
Stayman Winesap	Tenn.	
Sweet Winesap	N. Y.	
Tolman	Me., N. Y.	
Tompkin's King	N. S.	
Twenty Ounce	Me., Mass., N. Y.	
Wagener	Me., N. S.	
Wealthy	Ind., Mass., Me., N. Y., Tenn.	
Winesap	Ind., Me., N. Y., Tenn., Vt., Va., W. Va.	
Winter Banana	Ind., Me., N. Y.	
Wolf River	N. Y.	
Yellow Bellflower	N. S.	
Yellow Transparent	Md., N. Y., Tenn., N. S.	Va.
York	——	Va.

The species and genera of pomaceous hosts recorded above show no simple relationship or correlation by which one can formulate a rule to encompass them and set them apart from related non-susceptible plants. Nevertheless, they possess several distinctive features chiefly with respect to their taxonomy and their geographic range. Pomaceous hosts of *G. clavipes* are found in eleven genera. So far as I am able to learn no other species of *Gymnosporangium* is known to have hosts in so large a range of genera. All of the host genera of *G. clavipes* are closely related, however, and confined within the family Rosaceae. The native geographic range of these hosts is more extensive than for those of any other species of *Gymnosporangium* known to me. Pomaceous hosts of *G. clavipes* are found throughout the whole of the temperate portion of the northern hemisphere.

One of the most outstanding of the introduced foreign host species to become parasitised is *Cydonia oblonga,* the quince. This plant is native over the greater portion of Asia but has been introduced into North America over a portion only of the range of the rust. In the genus *Chaenomeles,* also native to Asia, two of the three species listed in Rehder's Manual are attacked. Several varieties and forms of the Japanese quince (*Chaenomeles* spp.) are also parasitised. One European and one Asiatic species of the genus *Pyrus* are attacked, while all other species (Eurasian) have so far proved to be immune. Some native and some foreign species of *Malus* as well as many orchard varieties of apples are

hosts to *G. clavipes*. In the genus *Sorbus* the two North American species are susceptible while all of the foreign ones inoculated remained immune. The hybrid genus *Amelosorbus* has but one species susceptible to *G. clavipes*. All of the species of the genus *Aronia*, native to North America, are hosts. With the exception of three or four species the genus *Amelanchier*, as represented in North America, is attacked by *G. clavipes*. A single species of the genus *Photinia*, the Eurasian species *P. villosa*, is liable to infection.



% suscept.	100	100	100	100	96	94	88	84	83	75	74	68	67	67	67	63	50	50	50	42	00
No. sp. with frt. tested	21	19	8	1	24	78	32	31	30	52	35	59	9	3	3	63	14	2	2	12	1
No. hosts.	21	19	8	1	23	73	28	26	25	39	26	40	6	2	2	40	7	1	1	5	0
Approx. no. sp. in group.	?	27	11	1	61	120	51	151	59	122	62	143	37	4	4	125	79	3	51	86	2

FIGURE 1. Data on Species and Varieties in Groups of the Genus *Crataegus* Susceptible to Attack by *Gymnosporangium clavipes* C. and P.

The susceptibility of each group of the genus *Crataegus* is presented as a graph in figure 1. The data for this graph were obtained by determining the percentage relationship between the number of species and varieties tested and the number that proved to be susceptible. While little significance can be attached to the results obtained from groups with a small number of species and varieties, nevertheless, reliable deductions can be made from those with large numbers as well as from the genus as a whole.

Susceptible species were found in all groups except the Bracteatae. Unfortunately this group was represented in the Arnold Arboretum by but a single tree. In these investigations, 79 per cent of the species that produced fruit when the tests were made proved to be susceptible. Many species and varieties have not yet been tested, either because they were not available or because they did not produce fruits in the years of my

investigations. Therefore, the host list is far from complete. All of the foreign species and varieties available for testing (placed in the group Oxyacanthae) proved to be susceptible. Of the native *Crataegi,* the percentage of species susceptible in the several groups varied widely. In some groups, for example, the Anomalae and Douglasianae, all of the species and varieties tested were susceptible while in other groups, for example, the Molles, Virides and Flavae, the percentage of susceptible members was less. It is interesting to note that the relative susceptibility of species and varieties and of the groups of the genus is not the same for hosts of *G. clavipes* as MacLachlan (1935) found for hosts of *G. globosum,* though hosts for both of these fungi were in most cases determined from the same individual trees.

III. PRELIMINARY STUDIES ON THE PERIOD OF SUSCEPTIBILITY OF POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES

It has been shown by several investigators that the leaves of pomaceous hosts of certain species of *Gymnosporangium* are susceptible during a limited period in their youth only. This interim is known as the period of susceptibility. Thomas (1933) showed that leaves of *Crataegus* spp. were susceptible in their youth only to the attack of *G. clavipes.* My preliminary investigations, with respect to this phenomenon on fruits of pomaceous hosts of *G. clavipes,* also indicate that their period of susceptibility is brief. In this connection inoculations were made every two days for a period of four weeks on different fruit clusters of two species of *Crataegus, C. tomentosa* and *C. fertilis.* Experimentation began when the flower buds of each species were opening. On *C. tomentosa* the ovaries, calyces, petals, pedicels, peduncles and twigs were attacked before the flowers opened. All but the ovaries and young fruit became immune within ten days. The fruits became decreasingly susceptible and by the time the petals fell they could no longer be infected. On *C. fertilis,* the young fruits only became infected. The flowers were immune up to the time the buds were opening and the petals began to expand; they then entered a brief period of susceptibility extending until the time when the petals began to fall, after which they again became immune.

A measure of susceptibility of the hosts of *G. clavipes* is here suggested. Those hosts that are susceptible for a longer period may be considered to be more susceptible than those that can be infected for a shorter period. No consistent difference was observed with respect to the abundance of aecia produced on susceptible as compared with resistant hosts.

The possibility of any relationship between immunity and fertilization was not investigated.

IV. THE JUNIPERUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P., THEIR TAXONOMIC POSITIONS AND THEIR GEOGRAPHIC RANGE

Cultural studies for the purpose of determining the Juniperus hosts of *G. clavipes* have been very limited indeed. Arthur (1912) cultured *G. clavipes* on *J. communis depressa* Pursh (*J. sibirica* Burgsd.) and Dodge (1918) obtained heavy infection from sowing aeciospores of *G. clavipes* on *J. virginiana* L. Several other investigators have substantiated these reports and added other hosts from their field observations. In my own work I have repeatedly cultured this rust on the red cedar, *J. virginiana* L. The technique for this work followed essentially the same procedure as for culture work on pomaceous plants. A complete enumeration (to 1934) of the Juniperus hosts of *G. clavipes* together with data on their taxonomic position, as given by Rehder (1927), and their geographic range are presented in table 3. I have examined the rust on all of these species and varieties.

TABLE III. JUNIPERUS HOSTS OF G. CLAVIPES

Juniperus hosts	Taxonomic position	Geographic range
J. communis L.	Oxycedrus	North Amer., Eurasia
var. depressa Pursh.	"	" " "
var. hibernica Gord.	"	Europe
var. montana Ait.	"	North Amer., Eurasia
J. horizontalis Moench	Sabina	" "
J. Sabina L.	"	Europe
J. scopulorum Sarg.	"	Western North Amer.
J. virginiana L.	"	Eastern North Amer.

In 1933 each individual cedar in the collections at the Arnold Arboretum of Harvard University was examined for infection and the species and varieties were recorded in immune and susceptible groups. The species and varieties of *Juniperus* on which no infection was observed are as follows:

Juniperus chinensis L., *J. chinensis globosa* Hornibrook, *J. chinensis japonica* Lav., *J. chinensis mas* Gord., *J. chinensis pendula* Franch., *J. chinensis Pfitzeriana* Spaeth, *J. chinensis plumosa* Hornibrook, *J. chinensis plumosa aurea* Hornibrook, *J. chinensis pyramidalis* Beiss., *J. chinensis Sargentii* Rehd., *J. chinensis Watereri* Hort., *J. communis Ashfordii* Hort., *J. communis aurea* Nichols., *J. communis aureo-spica* Rehd., *J. communis compressa* Carr., *J. communis cracovica* Hort., *J. communis oblongo-pendula* Sudw., *J. communis oblonga* Loud., *J. com-*

munis pyramidalis Hort., *J. communis suecica* Ait., *J. conferta* Parl., *J. formosana* Hayata, *J. horizontalis alpina* Rehd., *J. horizontalis Douglasii* Rehd., *J. horizontalis glomerata* Rehd., *J. horizontalis plumosa* Rehd., *J. horizontalis variegata* Hort., *J. procumbens* Sieb., *J. rigida* Sieb. & Zucc., *J. Sabina cupressifolia* Ait., *J. Sabina pyramidalis* Hort., *J. Sabina tamariscifolia* Ait., *J. Sabina variegata* Carr., *J. scopulorum horizontalis* D. Hill, *J. scopulorum viridifolia* Hort., *J. squamata* Buch.-Ham., *J. squamata Fargesii* Rehd. & Wils., *J. squamata Meyeri* Rehd., *J. squamata Wilsonii* Rehd., *J. virginiana aurea* Hort., *J. virginiana Burkii, J. virginiana Canaertii* Senecl., *J. virginiana Chamberlaynii* Carr., *J. virginiana cinerascens* Hort., *J. virginiana elegantissima* Hochst., *J. virginiana fastigiata* Hort., *J. virginiana filifera* D. Hill, *J. virginiana glauca* Carr., *J. virginiana globosa* Beiss., *J. virginiana Hillii* Hort., *J. virginiana Kosteri* Beiss., *J. virginiana pendula* Carr., *J. virginiana polymorpha* Hort., *J. virginiana pyramidalis* Carr., *J. virginiana pyramidalis glauca* Hort., *J. virginiana plumosa* Rehd., *J. virginiana reptans* Beiss., *J. virginiana Schottii* Gord., *J. virginiana tripartita* R. Smith and *J. virginiana venusta* Rehd.

Usually the Juniperus hosts of species of *Gymnosporangium* are confined to a single section of the genus. Those of *G. clavipes* are exceptional in that they are classified in two sections of the genus, Sabina and Oxycedrus. Geographically the Juniperus hosts of *G. clavipes* are found throughout the greater portion of the temperate region of the northern hemisphere, an unusually wide distribution for telial hosts of any one species of *Gymnosporangium*.

V. SYMPTOMATOLOGY OF THE DISEASES CAUSED BY GYMNOSPORANGIUM CLAVIPES

1. On Pomaceous Hosts

(A) Morphological symptomatology

Morphological symptoms of disease caused by *G. clavipes* were first described from infected fruits on pomaceous hosts. Schweinitz (1832) gave a brief description of the gross morphological symptoms of the disease on the fruit of *Crataegus* sp. Farlow (1880) stated that *G. clavipes* (*Roestelia aurantiaca*) was "by far the most beautiful species of the genus which we have, at once attracting the popular eye by its brilliant orange or almost cinnabar colored spores and shining white peridium. It is generally found on young fruit, though it is occasionally found on the stems and petioles, but I do not recollect having seen aecidia on the leaves. — One sometimes sees a quince two inches in diameter

more than half covered by the bright orange aecidia and occasionally small apples are affected in a similar way. *Roestelia aurantiaca* is generally found in midsummer. I have, however, seen it on *C. crus-galli* as late as October."

Weimer (1917) stated that "the veins alone (of quince leaves) are attacked and often become swollen to double their normal size." The swellings, he noted, caused the leaves to curl but the infected areas were not discolored. No aecia were found on the quince leaves. Adams (1921) reported that branches and buds of hawthorns were very severely injured by this rust. He stated that "the aecia on the branches always precede the appearance of aecia on the fruit of hawthorns." Thomas (1933) reported that symptoms on apple foliage appeared 10 to 18 days after inoculating and that on apple fruits the symptoms were predominately necrotic or hypoplastic. On artificially inoculated leaves of *Crataegus* he obtained numerous spermogonia "but aecia were produced only sparingly along the larger veins."

In the present study, data for the symptomatology of the disease caused by the aecial phase of *G. clavipes* were obtained from observations made on more than 400 pomaceous hosts. Data on the relationship between elapsed time and progressive stages of development of symptoms and signs were recorded from plants inoculated at various stages of development of the flowers, twigs and fruits. Comparisons of the symptoms and signs resulting from artificial inoculations made possible a more thorough understanding of the phenomena that occur in nature.

Gymnosporangium clavipes attacks primarily the fruits, less frequently the twigs and buds and rarely the leaves of its pomaceous hosts. The earliest observable symptom of disease on ovaries and young fruits is a pale yellowish green discoloration. This symptom was seen on certain species even before the petals fell. Occasionally the petals become infected and when they do they usually remain attached for the greater part of the season. In my experience, fruits are susceptible when in early stages of development only. After the petals drop the fruits of most species are no longer subject to infection. On the average, from 6 to 10 days after inoculating the diseased fruits begin to show evidence of infection by slightly pale swellings. From 4 to 5 days later the hypertrophied zone becomes dotted in its central portion with numerous, tiny, deep-reddish points — the developing spermogonia of the fungus. Within 1 to 5 more days, the first formed spermogonia begin to exude a pale-red, sweetish liquid. During further development the diseased area continues to increase in all dimensions and finally involves but a portion of, or, in many cases, the whole fruit. Occasionally, the infection spreads to the pedicels and even extends into the peduncles and twigs. Spermo-

gonia are matured progressively over a large portion of the diseased tissue, and oozing of the young spermogonia continues for several days. The older spermogonia die and turn black.

Several irregularities or anomalies have been observed in the symptomatology of the disease during the life span of the spermogonia. Very frequently the infected tissues do not become hypertrophied, but quite cease development. During this time the adjacent tissues continue to expand, resulting in invaginated areas. This is particularly common in orchard apples where infection occurs most frequently at the blossom end. In many instances the spermogonia are few in number and do not reach full maturity. Tissues with this type of infection are usually green and firm. Fruits of hawthorns, shadbushes and chokeberries are found in which the swelling and discoloration involve the whole fruit, but in such cases no or few spermogonia are produced. Many of the fructifications exhibit various stages of abortion. Symptoms of this type were obtained from inoculation tests on *Crataegus* spp. and *Amelanchier oblongifolia* toward the close of the period of susceptibility of the fruits. Of course, in some instances it is possible that more than one kind of parasite is involved and that as a result the normal course of the Gymnosporangium disease is altered.

In 20 to 40 days after inoculating the second fructifications of the fungus, the aecia, begin to make their appearance within the diseased area. They are usually produced peripheral to, or to one side of, the spermogonia; but they are often found among them. Aecia, in progressive stages of development, are easily observed during their early appearance as is shown in plate 155, fig. 1. Often no aecia penetrate the surface of the infected fruits, yet internal ones are frequently formed. This is particularly true of orchard apples but has also been observed in many other hosts. Fruits that become infected late in the period of susceptibility are commonly observed to exhibit this phenomenon. Failure to fully develop aecia may be physiological — possibly a type of hypersensitivity — or it may be due to the development of a cuticle so tough as to prevent aecia from breaking through.

Many fruits were observed in which the lesions occupied by *G. clavipes* were browned or blackened and quite rotted. From such decayed areas imperfect fungi were repeatedly obtained by culture. It seems, therefore, that these are the real cause of the discoloration and decay noted. Some have ascribed such phenomena to *G. clavipes*, but it seems erroneously so. The fact that relatively few areas infected by *G. clavipes* become decayed strengthens this conclusion. A photograph of a rust-infected area that was parasitised by an imperfect fungus is in plate 155, fig. 2.

An anomolous symptom was frequently observed on fruits of *Crataegus monogyna* infected with *G. clavipes*. The whole of the fruits and the pedicels were infected, but from the blossom ends of these fruits numerous petals and abortive structures resembling stamens developed. Here again, more than one parasitic organism may have been active in causing these symptoms.

Twigs, including thorns, infected with *G. clavipes* are commonly found on certain species of hosts (plate 156). In my experience twigs of the current season only have become infected. The early symptoms of disease on twigs are pale, yellowish green, elongated areas occurring on the young bark. The infection spreads rapidly, however, usually girdling the stem and extending up to 3 inches longitudinally. The infected portion of the twig becomes hypertrophied. Frequently a fusiform swelling results, but irregularly swollen and cankered twigs are also common. Rarely, however, rotund galls are formed on the twigs. Thorns are also subject to infection and manifest similar symptoms. Spermogonia on infected twigs usually do not reach maturity until 9 to 12 days after inoculation. They follow the same course of development as on fruits. Aecia of the rust are produced among the spermogonia as well as outside the area occupied by them. Very often they are sparsely produced, but, on the other hand, twigs are sometimes found in which the aecia are very abundant. The first aecia reach maturity on the twigs and thorns in 30 to 40 days; others are produced progressively, as was described in the case of infected fruits, for a period of about a week.

In the longitudinal advancement of the fungus in a twig, it frequently encounters a terminal or lateral bud, which in turn usually becomes infected. Subsequently, the buds are forced to develop beyond the resting stage normal for the current season. Similar phenomena were observed on buds of ornamental apples infected with *G. Juniperi-virginianae* (Crowell, 1934). Forced growth of buds caused by *G. clavipes* has been observed on a large number of hosts. The early stages of infection, evidenced by a yellow discoloration and swellings of the buds, are not observable until late in June. The abnormal development of stunted twigs and leaves results. The photographs in plate 156 show some of these symptoms in forced buds. Spermogonia in all stages of development are produced along the deformed petioles and veins of the leaves. Rarely, however, are aecia produced on the forced buds. On *C. Phaenopyrum* several twigs were found in which the infection developed systematically, as shown in plate 156, fig. 5. It is possible that infection occurred on these twigs while they were in the stage of rapid elongation. That infection was confined largely to these malformations and did not extend into the main twig substantiates this supposition.

Many twigs infected with *G. clavipes* in the spring of 1934 were examined in the spring of 1935 to determine whether or not the fungus overwintered in its aecial hosts. No instance of overwintering was found. Thomas (1933), however, reported having observed the overwintering of this rust in pomaceous hosts. Dodge (1918) reported that the aecial phase of *G. biseptatum* Ellis (*G. Botryapites* [Schw.] Kern) and of *G. fraternum* Kern (*G. transformans* [Ellis] Kern) were observed by him to be perennial. Tubeuf (1906, 1907) also noted this phenomenon on pears infected with *G. Sabinae* (Dicks) Wint.

The leaves of the pomaceous hosts of *G. clavipes* are rarely infected. When such occurs the lesions are always small and few spermogonia develop on them. The spermogonia on leaf lesions are late in appearing, and on many hosts they never reach the oozing stage. Spermogonia have been observed on leaves of *Cydonia oblonga, Amelanchier* spp., *Craetegus* spp., and *Aronia* spp. *Amelanchier oblongifolia* is the only host, however, in which I have seen aecia of *G. clavipes* on affected leaves.

On its more susceptible pomaceous hosts *G. clavipes* is very destructive. The diseased fruits become misshapen and discolored, and often fall prematurely. In the case of quince and apples the loss is primarily a commercial one and frequently very great. Indeed, growing of quinces was impossible in many sections of eastern North America due largely to the ravages of this rust. Many varieties of orchard apples are also very susceptible. Thomas and Mills (1930) report instances in which as high as 95% of the fruits of the Delicious variety in New York were attacked. Ornamental plants, such as certain species of *Crataegus, Amelanchier*, etc., whose beauty and usefulness depend in a large measure upon an abundant production of colored fruits that persist long into the winter, sometime becomes worthless because so many of their fruits are spoiled by *G. clavipes*. Twigs killed beyond the infected portion are also unsightly and they tend to materially deform the trees and shrubs because of sequent prolific sprout growth. Hawthorns have been seen in which so many twigs were killed by the rust that death resulted.

(B) Histological symptomatology

Tissues of pomaceous hosts infected with *G. clavipes* are usually hypertrophied and the diseased portions of fruits and twigs are often greatly enlarged; infected parts of leaves, however, are changed but little. In the fruits chiefly the outer or cortical tissues are affected. They are often greatly enlarged and many of them are more or less filled with a deep-staining material while others, fully as hypertrophied, are often quite devoid of contents. Cells towards the center of the fruit, although they show no evident hypertrophy, contain much of the deeply staining

material observed in the cortical cells. Exceptions to the hypertrophy of the fruit cells as noted have been observed in the infections of many orchard varieties of apples. In such infections the earliest stages of the disease are manifested as an hypertrophy of a small number of cells. The disease soon ceases to be an enlargement; indeed, the infected region becomes inhibited in its development. The surrounding uninfected tissues, however, continue to expand in their development while the diseased area remains stunted, depressed and usually greenish.

In twigs, mainly the cortical tissues are affected. The effects are similar to those in fruits. Occasionally, however, and always in the greatly enlarged twigs, the phloem and xylem are hypertrophied. Many of their cells contain much material that stains intensely with haematoxylin.

The mycelium of the aecial phase of *G. clavipes* is found in the cortical tissues of the fruits and twigs and in the palisade and mesophyll tissues of the leaves. Haustoria are abundantly formed in the cells of the fruits and twigs but are seldom seen in cells of the leaves. Frequently, haustoria are found in close association with the nucleus of its host cell.

The peridial cells and the aeciospores of *G. clavipes* are salient features for determination of the species. *Gymnosporangium clavipes* can also readily be identified from median longitudinal sections of the spermogonium. In my investigations of the spermogonia of the genus (to be reported in a separate article) three dimensions were averaged, namely, total width, total height and the depth to which the fructification is sunken in the host tissue. The measurements for *G. clavipes* were found to be 203 μ × 207 μ × 163 μ respectively. The spermogonia of *G. clavipes* are conspicuous because of their large size and their rotund form and they are almost completely sunken in the mesophyll. A photomicrograph of spermogonia of *G. clavipes* is shown in plate 156, figure 7.

Aecia of *G. clavipes* are found most abundantly in the fruits and twigs and are seldom produced in the leaves. Aecia develop in the outer cortex of fruits and twigs and in the mesophyll of leaves. They are sunken to a depth of approximately one millimeter and are of greater diameter near the base than at the apex. Fresh aeciospores of *G. clavipes* vary in color from bittersweet-orange to flame-scarlet (Ridgway, 1912). They are irregularly rotund, verruculose and measure 32.2 μ × 34.4 μ. Peridial cells are almost white in color; the inner wall is maked by coarse ridges forming an irregular mosaic pattern. The form of peridial cells varies widely, but on an average they measure 14.5 μ in width × 55.6 μ in length. They usually adhere in large numbers in water mounts.

2. On Juniperus Hosts

(A) Morphological symptomatology

Cooke and Peck (1873) gave a description of the symptoms of *G. clavipes* on *Juniperus virginiana;* they stated: "the younger branches are slightly swollen where attacked by this fungus and the bark is scaly." For many years, however, the fungus and the disease caused on its Juniperus hosts seem not to have been understood. Thaxter (1891) after an extensive series of cultural experiments clearly identified two species that were formerly confused with *G. clavipes,* namely *G. clavipes* proper and a new species, *G. Nidus-avis.* Kern (1911), in an account of the symptomatology of *G. clavipes,* stated that the telia were "caulicolus, appearing on slightly fusiform swellings, usually aggregated, roundish, one to four millimeters, often confulent, hemispheric — teliospores two-celled ellipsoidal 18 to 26 μ × 35 to 51 μ — pedicels carotiform. Dodge (1918) stated that small witches-brooms are sometimes formed on twigs of red cedars infected with *G. clavipes.* Dodge (1922) stated that needles as well as the main trunk are also infected, and that the bark over the infected portions of the trunk becomes much thickened and blackened.

The pertinent observations on the symptomatology of *G. clavipes* reviewed in the foregoing give a clear foundation for an appreciation of the disease caused by *G. clavipes* on its Juniperus hosts. My own findings and interpretations, while they add little to what is already known will, nevertheless, trace in sequence the development of the disease and its relative importance in the various organs attacked.

On its Juniperus hosts, particularly *J. virginiana* L., the disease induced by *G. clavipes* is perhaps one of the most destructive caused by any species of the genus *Gymnosporangium.* The needles, twigs, branches and even the main trunk are attacked. Very frequently the disease occurs on the needles but infected needles are relatively inconspicuous and are often overlooked. Usually but a single crop of teliospores is produced on needles, after which they die. From the needles, however, the fungus often migrates to the twigs and it is on these that the disease is most frequently found. Twigs may also become infected directly. On twigs the disease appears as slightly fusiform swellings covered by a flaky, darkened bark. Usually by the end of four to six years most of the infected twigs die. Occasionally, however, the infected twigs survive for a longer period and the larger limbs are distorted and covered with a heavy, cracked and blackened bark. If the diseased portion of a branch is near the main trunk the latter is liable to infection by the fungus advancing along the cortex. Infections of *G. clavipes* on the

main trunk of red cedars are easily mistaken for one of the diseases caused by other species of the genus, because vertically elongated, often irregular, blackened, heavy-barked bulges are typical for diseases caused by several species of *Gymnosporangium*. Fructifications are, in my experience, necessary to identify the causal organism on trunk lesions.

That the disease caused by *G. clavipes* is very destructive to its telial host is evident since all organs attacked are killed usually in a few years. Trunk infections of many years standing are not uncommon, to be sure; but trees bearing such burdens show evident symptoms of poor health. Recently, I came upon a very striking demonstration of destruction of red cedars infected with *G. clavipes*. Several years ago, an estate owner cleared a natural grove of cedars of all other trees and shrubs. *Gymnosporangium clavipes* was very abundant on the twigs, branches and main trunks of certain of these cedars. Following the unusual cold of the winter of 1933-34 every tree that was heavily infected with *G. clavipes* died entirely or in large part, while all of the trees in this group that were not infected survived. An examination of the cedars in the surrounding uncleared lands revealed complete destruction of trees that were heavily infected with *G. clavipes*. As the only variable seemed to be the relative abundance of infections the loss seemed clearly attributable to the infection of *G. clavipes*.

(B) Histological symptomatology

Dodge (1922) gave a very complete account of the histological symptomatology of *G. clavipes*. A review of his paper is presented here. Dodge stated that "infection takes place on the proaxial side of the young leaf, or directly on the young stem at the base of the leaf — after entering the leaf, the mycelium invades the region between the cuticle and the cellulose walls of the epidermis on the proaxial side. The effect of the fungus on this part of the cell wall is usually marked by considerable swelling and the disorganized substances take the stains very readily — the fungus explores and feeds in the cuticularized layer, but it may go deeper and invade the palisade-mesophyll tissue. Haustoria are found in the epidermal cells, sometimes even in the guard cells of the stomata."

Young stems are "susceptible to infection, either directly or through the invasion of the fungus by way of the leaf axils." The mycelium occupies a cancellate portion of the periphery of the young cortex. The mycelial "strands actually interlace, weaving in and out around the veins [leaf traces] of the leaves and forming a closed network system in the cortical region of the young stem." After the leaves are shed the fungus, closing the gaps, may be found in the cortex around the entire circum-

ference of every section. In the main trunk, infections are confined to a portion only of the circumference.

My findings with respect to the histological symptomatology agreed in detail with those of Dodge. My examination included the leaves and twigs of *Juniperus virginiana* as well as infected twigs of all other Juniperus hosts. Certain additional remarks with respect to the fructifications are also recorded.

The telia of *G. clavipes* arise at irregular intervals from aggregated masses of the mycelium on the phellogen. The telia first appear early in April in Massachusetts. In youth they are a deep-reddish color, expanding upon gelatinization to regular pulvinate sori. After two or three gelatinizations, however, the sori change their deep red color to a yellowish red and their shape is very irregular. Five to six gelatinizations occur during the season, after which the telia drop from their host.

VI. LIFE HISTORY STUDIES OF GYMNOSPORANGIUM CLAVIPES C. AND P.

The life history of *Gymnosporangium clavipes* is essentially the same as that of other species of the genus. It differs in certain details only from the life history of the more generally known species *G. Juniperi-virginianae*. A review of the extensive literature dealing with the life-history of *G. clavipes* shall be confined to the more pertinent reports of former investigators.

Schweinitz (1832) described the aecial phase of a rust which he found occurring "rarissime in germinibus Rosae" as *Caeoma* (*Peridermium*) *germinale*. Kern (1911) reported the determination of the host of this rust to be an error for a species of *Crataegus*. Cooke and Peck (1873) gave an account of the telial phase of a rust which they called *G. clavipes* occurring on *Juniperus virginiana* L. These two rusts were considered to be distinct species until Thaxter (1887) showed from the results of controlled cultural experiments that the spermogonial and aecial stages on pomaceous hosts were in reality genetically connected with the telia stage on red cedars. Following this basic step many observations have been reported with respect to details in the life history of *G. clavipes*.

In the development of the rust on pomaceous hosts Farlow (1886) and Thaxter (1887) found that 10 and 11 days respectively elapsed between the date of inoculating and the first appearance of spermogonia. Thomas (1933) stated that the first symptoms of disease on "relatively resistant" apple foliage were observed 10–18 days after inoculating but that spermogonia were never formed on the lesions. In contrast he found that symptoms appeared in 4–6 days and spermogonia in 13–15 days after

inoculating "susceptible" foliage of *Crataegus* sp. and further that aecia were formed sparingly along the larger veins only of the infected leaves. Thaxter (1887) determined from his cultures that approximately 30 days were required for the maturation of aecia on young shoots of *Amelanchier canadensis*. Miller (1932) and other authors observed that spermogonia were frequently abortive in orchard apples and that aecia rarely matured in the fruits.

These observations while they differ greatly when considered separately are nevertheless in harmony when reviewed in the light of more complete knowledge of the behavior of the rust. From my cultural experiments on hosts in several genera, the same variations as reported in the foregoing were observed. These variations seemed to be correlated with two phenomena, — first, the relative susceptibility of the host plants and second, the stage of development of the diseased parts at the time of inoculating. The rust developed more rapidly on the more susceptible hosts and more slowly on less susceptible ones. In fact, on very resistant hosts, as certain orchard apples or on resistant organs as, for example, the leaves of nearly all hosts, longer time was required for the maturation of the fructifications; not infrequently these reached an imperfectly developed stage only.

The average time required for the maturation of spermogonia of *G. clavipes* on fruits and twigs was from 7 to 10 days. The beginning of spermogonial exudation was taken as the criterion of maturity. On individual lesions spermogonia continued to be produced for a period up to 3 weeks. The production of exudate by any one spermogonium continued up to about 7 days, after which the spermogonium became filled with long filaments, and soon died, usually turning black. Others in the lesion followed these developments. Spermogonia of *G. clavipes* were sub-epidermal in origin and position; they were reddish in color and among the largest of the genus. Details of average measurements of their size have been given on page 385.

The aecial primordium of *G. clavipes* is located deep in the cortical tissues of fruits and twigs and in the mesophyll of leaves. It is typical for the genus as is also the mycelium and haustoria. From thirty to forty days after inoculating, aecia of *G. clavipes* reached maturity and penetrated the epidermis of the host among or close by the spermogonia. Aecia were usually developed progressively over a period of a week or more. Upon their first appearance, about June 1 in Massachusetts, they had the form of short, blunt, white cylinders. One or two days later the white peridia were ruptured irregularly, usually with the loss of the cap cells, exposing and releasing the enclosed reddish aeciospores. Vari-

ous stages of this phenomenon are shown in plate 155, fig. 1. The aecium of *G. clavipes* is broader at about midway between the hymenium and surface of the host than at the surface of the host itself. It is evident, therefore, that a crowding of the aeciospores occurs at the zone of constriction. Dodge (1924) associates these phenomena with a mechanism for the forcible discharge of aeciospores.

The peridial cells of *G. clavipes* are broadly rectangular and measure 14.5 μ × 55.6 μ with extremes of 33.4 μ to 83.5 μ × 10.4 μ to 23.4 μ. Their inner and thicker walls are ornamented with low interconnecting prominences forming irregular mosaic patterns. Peridial cells are of much diagnostic value as Fischer (1891) and Kern (1910) demonstrated. Those of *G. clavipes* may be easily identified by their markings, their size and their form. Peridial cells of *G. clavipes* usually remain flat in water mounts and adhere forming a large sheet of cells.

Aeciospores of *G. clavipes* are exceptional for the genus in their remarkably intense color. By comparisons of fresh aeciospores the color was determined as varying from bittersweet-orange to flame-scarlet according to Ridgway's (1912) color standards. With increase of age of the mature spores, however, their color gradually changes to orange and yellows. In old herbarium material they are frequently almost colorless. In many of the better preserved specimens the reddish color still is conspicuous. Aeciospores of *G. clavipes* are among the largest of the genus. They measure 32.2 μ × 34.4 μ with extremes of 28.4 μ to 42.3 μ × 26.7 μ to 37.4 μ. Their outer surfaces are ornamented with numerous, tiny, low papillae.

The problem of germinating aeciospores of species of *Gymnosporangium* has been given a great deal of attention. Difficulty has been experienced in germination of aeciospores of many species. Several investigators have shown that a period of rest at low temperature contributed greatly to the germinability of aeciospores of certain species of *Gymnosporangium* (Fukushi, 1925; Miller, 1932). Thomas and Mills (1929) reported moderate germination of aeciospores of *G. clavipes* stored for twelve weeks at 3° C. Thomas (1933) tested the germinability of aeciospores of *G. clavipes* that were precooled for various lengths of time at various temperatures as well as aeciospores that were not precooled. The highest germination was obtained from spores that "were mounted at 18° C. without precooling." Thomas also demonstrated that aeciospores kept dry at 3° C. rapidly lost the property of germination. It was found, however, that a small number of aeciospores remained viable in aecia in fruits throughout the winter. It should also be remarked that Professor J. C. Arthur observed internal aecia of *G. clavipes*

in fruits of orchard apples. Dr. Arthur stated in a letter to Dr. Steinmetz, who forwarded the material to him, that aeciospores removed from internal sori germinated in the usual manner.

In my studies of the germination of aeciospores of *G. clavipes* it was found that they germinated readily in a moist atmosphere at room tem-

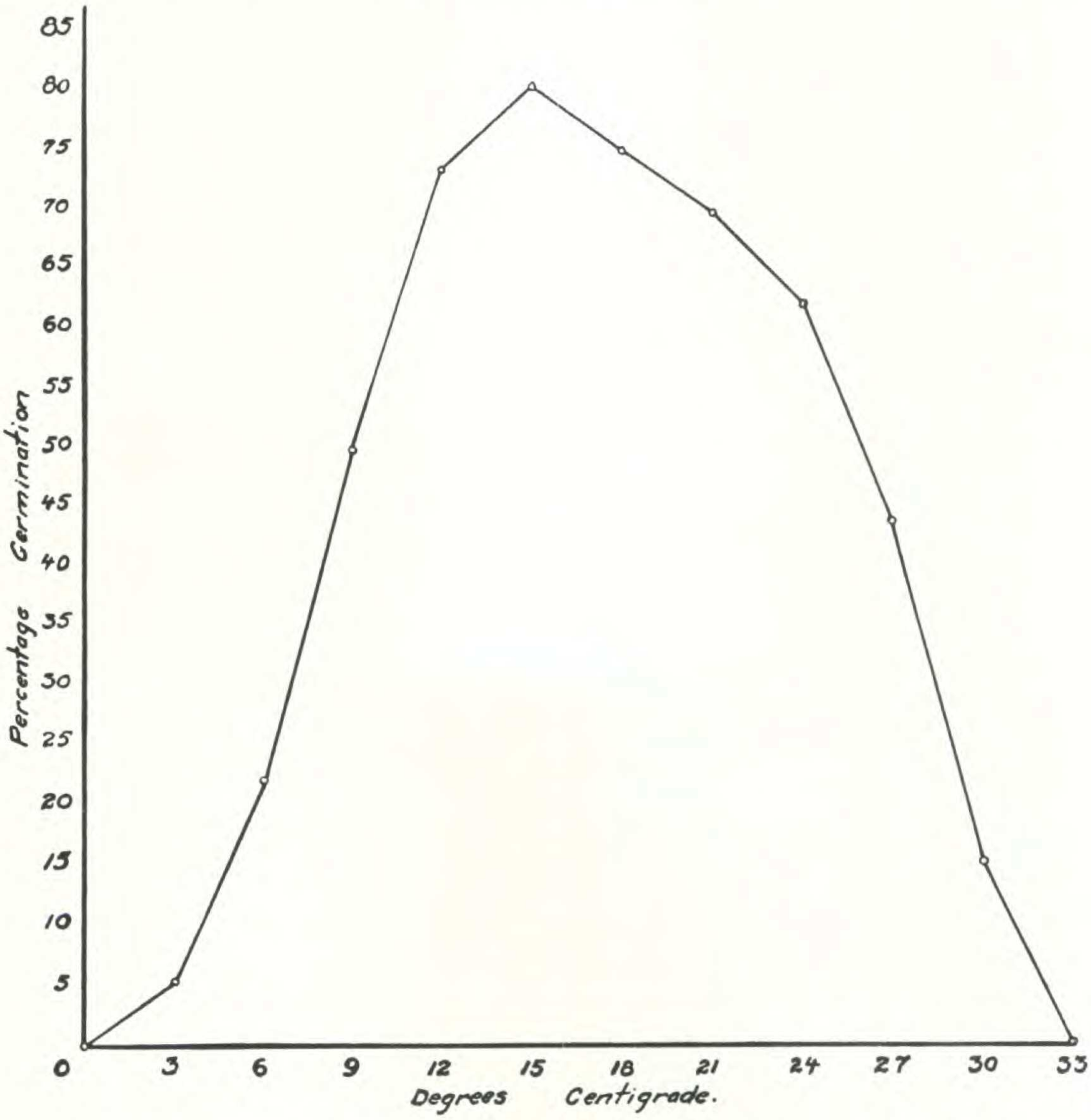


FIGURE 2. Graph showing the Germination of Aeciospores of *Gymnosporangium clavipes* C. and P.

perature at any time during the summer and fall seasons. Careful studies of germination revealed that they germinated over essentially the same range as did most species of the genus studied to date. Optimum conditions for germination in distilled water on glass slides were reached at about 15° C. The results of the tests are shown in figure 2 and in table 4.

TABLE IV. GERMINATION OF AECIOSPORES OF G. CLAVIPES

Temp.	No. of spores counted	No. of spores germinated	Percentage of germination
0° C.	1000	0	0
3	1000	53	5.3
6	1000	224	22.4
9	1000	506	50.6
12	1000	740	74.0
15	1000	807	80.7
18	1000	750	75.0
21	1000	698	69.8
24	1000	625	62.5
27	1000	413	41.3
30	1000	152	15.2
33	1000	0	0

Apart from the irregularities in the aecial phase that were discussed under the heading of symptomatology, an unusual development was observed in the aecia on fruits of *Crataegus* sp. collected by Prof. J. H. Faull in Pennsylvania. Some of these aecia and aeciospores appeared normal in all respects. Certain of the aecia were internal with the hymenia oriented in various directions. All of these latter and many of the aecia that developed in a normal position were filled with irregularly produced aeciospores and aeciospore chains. Cytologically either one or two nuclei were present in the cells. The cell contents were irregularly interspersed with vacuoles and deep-staining materials. Camera lucida drawings of two aeciospore chains are shown in plate 157, figure 2.

Aeciospores of *G. clavipes* are primarily wind borne. They are distributed throughout the growing seasons and probably germinate and infect the alternate hosts shortly after inoculation.

Previous to 1910, however, little investigative work had been conducted on the telial phase of *G. clavipes*. Arthur (1912) sowed aeciospores of *G. clavipes* on the common juniper and reported successful cultures. Dodge (1918) traced the life cycle of *G. clavipes* under controlled conditions from the telial phase on red cedars to the aecial phase on *Crataegus Oxyacantha*, thence back to the telial phase on red cedars. Dodge found that few telia were produced in the spring following inoculation but that many developed in the second spring. Inoculations made during the present investigations substantiated these findings. In addition it was shown that inoculations made on July 1, August 10 and October 3 all resulted in abundant infection, indicating that in nature aeciospores are a menace throughout their entire period of production.

Infection of the telial host was first described by Dodge (1922).

Dodge stated that entrance of the germ tube was gained through the adaxial surface of the leaves and tender epidermis of the twigs. In the leaves of its Juniperus hosts the mycelium of *G. clavipes* is confined almost exclusively to the epidermal cells. In twigs it is restricted to the phellogen cells — a most unusual limitation for the mycelium of a species of *Gymnosporangium*. Within the infected cells characteristic, binucleate, sac-like haustoria are formed. They are abundant, usually occurring singly but frequently in twos or threes. Telial sori of *G. clavipes* arise from masses of the mycelium. In leaves the mycelium usually dies after the production of one crop of spores, but in twigs the fungus is perennial for several years. After each successive crop of teliospores a new phellogen layer is formed immediately beneath the sorus. The surrounding vegetative mycelium then grows over this new tissue. It is from the mycelium on the older phellogen that the telium for the ensuing spring is produced. In certain microscopic sections it is possible to observe progressively (a) the dead mycelium on partially sloughed-off phellogens, (b) sori of the present season as well as (c) the primordia of sori for two seasons to come. The camera lucida drawing in plate 160, fig. 1 was made from such a section.

Telia of *G. clavipes* are produced on leaves and on the bark of various-sized branches and even the main trunk of red cedars. They were never observed on branches of red cedars more than one-half inch in diameter. Upon their early appearance telia of *G. clavipes* are aggregated, pulvinate in form, 2 to 5 mm. across and are distinctly bright reddish in color. During rains in the spring the telia swell to regular gelatinous forms as is shown in plate 159. After three or four gelatinizations the telia lose their regular form and deep-red color, becoming shapeless yellowish-red masses. After 6–8 gelatinizations the telia drop from the infected parts.

The development of teliospores of *G. clavipes* is essentially the same as Dodge (1918, 1922) reported for this and other species of the genus. Camera lucida drawings made during these investigations of teliospores in various stages of development are shown in plate 160.

Teliospores of *G. clavipes* are at once distinguished by the swollen pedicels near their bases. No other species of the genus in eastern North America has this characteristic. Certain data in regard to teliospores of *G. clavipes* are of interest. Both one- and two-celled teliospores are produced. In a count of 1000 spores, 94.8% were found to be two-celled while 5.2% were one-celled. Two-celled teliospores have one germ pore in each cell. In the upper cell the germ pore is apical while in the basal cell the germ pore is located near the pedicel. In other respects one-

celled teliospores resemble the two-celled ones in all but the septum. One-celled teliospores have the germ pore at the apex. In the telium of *G. clavipes* both thick- and thin-walled spores were found. Thick-walled spores are more numerous and are always produced on the outer surface of the telium. Almost invariably one-celled teliospores are thick-walled. Thin-walled teliospores are located within or beneath the layer of thick-walled spores. Measurements were made of the lengths of the upper and basal cells, the total length and the width of teliospores of *G. clavipes*. The upper cell measured 23.0 μ with extremes of 16.5 to 33.0 μ, the basal cell 21.2 μ with extremes of 14.9 to 33.0 μ, the total length was 44.5 μ with extremes of 33.0 to 57.8 μ and the width 22.7 μ with extremes of 16.5 to 33.0 μ. Single-celled spores measured 19.7 μ in width by 33.4 μ in length with extremes of 26.4 to 51.2 μ × 14.9 to 29.7 μ.

When teliospores of *G. clavipes* first break through the cortical covering layer of the host, they expand but little when wetted and the teliospores do not germinate. From 1–3 weeks after their first appearance, however, the telia expands fully to a regular pulvinate form and the teliospores germinate in great abundance.

Several workers have reported the results of their investigations on germination tests of teliospores of *G. clavipes*. Weimer (1917) formulated a general curve of germination percentages obtained at various temperatures and stated that it applied to the germination of teliospores of *G. clavipes* as well as teliospores of other species of *Gymnosporangium*. The extreme temperatures found by Weimer were 7° C. and 29° C. and the optimum temperature was between 22° C. and 25° C. Miller (1932) found the extreme temperatures of germination to be 4° C. and 32° C. and the optimum germination at 25° C. He also investigated the phenomenon of the maximum rate of germination and found that when telia of *G. clavipes* were immersed in water for 25 minutes and removed to a moist atmosphere they discharged basidiospores in considerable numbers within two hours. It was also found that when telia were mounted in moist cotton and kept at 25° C. an abundant germination of the teliospores and the beginning of basidiospore formation occurred after an interval of eight hours.

Thomas also investigated the time required for and the rate of germination of basidiospores. He stated that basidiospores submerged in water at room temperature developed germ tubes equal in length to the spore in two hours and from four to six times their diameter in ten hours. Basidiospores were also mounted on a moistened leaf of *Crataegus* and held at 25° C. with the result that germ tubes reached a length of five to seven times their diameter in eight hours.

Farlow (1886) reported the production of secondary basidiospores from primary basidiospores of *G. clavipes*, a phenomenon that has frequently been reported for other species of the genus.

Beyond observing the usual germination of the teliospores of *G. clavipes*, a process common to other species, no further studies were made on the phenomenon. It was observed, however, that germination occurred in the field when the telia remained gelatinized for periods of

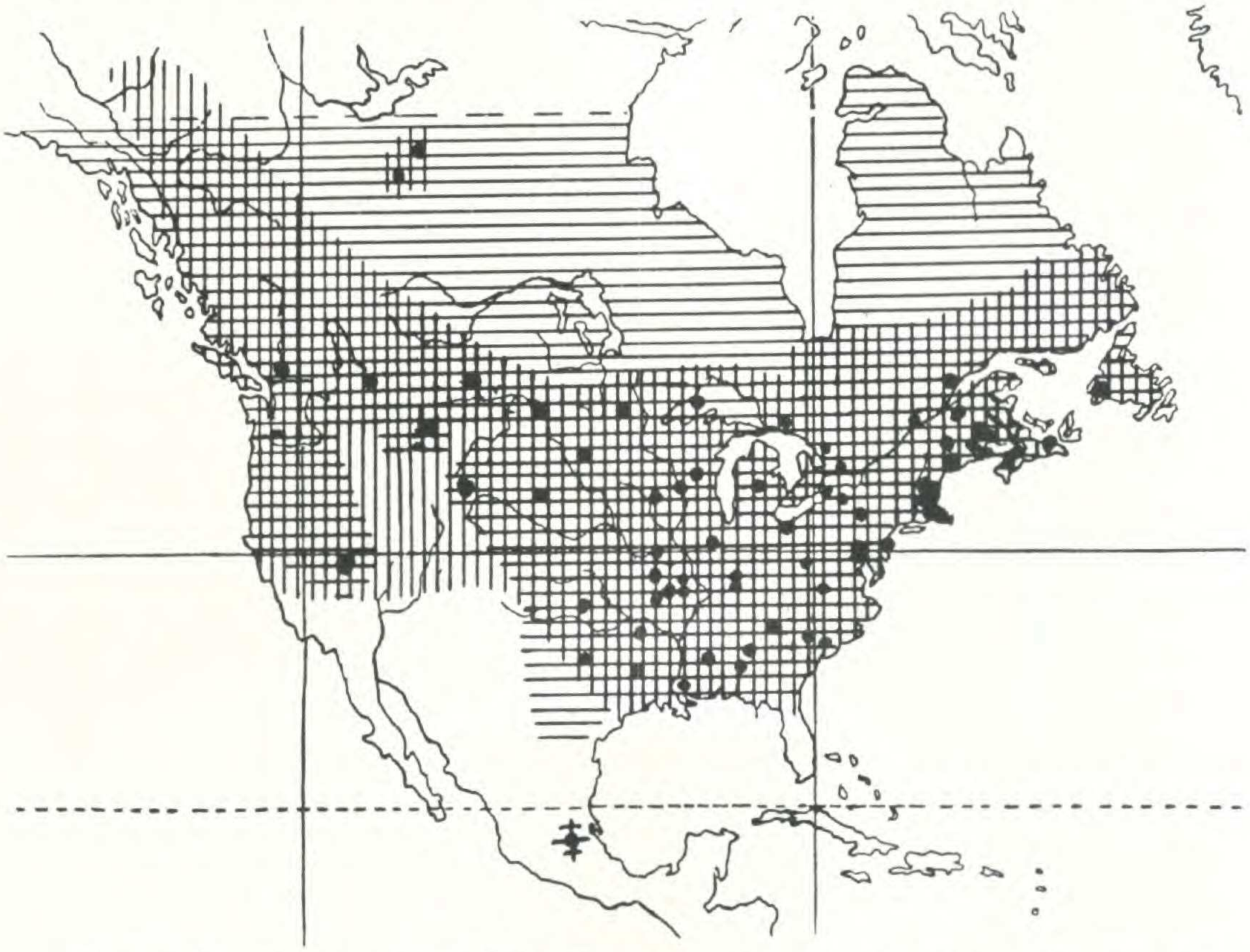


FIGURE 3. Geographical Distribution in North America of *G. clavipes* and its Hosts. The pomaceous hosts of *G. clavipes* shown as vertical lines. The Juniperus hosts of *G. clavipes* shown as horizontal lines. Stations for *G. clavipes* shown as dots. Note the extreme northern limit in northern Alberta, Canada, and the extreme southern limit near Mexico City, Mexico.

two hours or longer. Four to six gelatinizations were usual during the season and basidiospore dissemination occurred at most, if not at all, of these.

It is essential to the production of infection that the pomaceous hosts are within their period of susceptibility at the time of inoculation. As the period is very short in many species, the failure for the coincidence of basidiospore dissemination within this period may be held responsible for the variable abundance of spermogonia and aecia on certain pomaceous hosts in different years. Crowell (1935) reported unusual de-

velopments of the aecial phase of this and other species of *Gymnosporangium* in the very dry spring of 1935. In the spring of 1935, no rains sufficient to cause gelatinization of telia of *G. clavipes* occurred during the flowering period of most pomaceous hosts; most fruits becoming immune before inoculation took place. This resulted in a very limited number of infected fruits and the late appearance of the rust generally.

Although the host relationships for the perpetuation of *G. clavipes* are found over the greater part of the temperate northern hemisphere, nevertheless, so far as I am able to learn, this rust is not known outside of North America. Reported stations for this rust are most abundant in the eastern part of this continent as shown by dots on the outline map of North America in fig. 3. The rust has been collected, however, in widely separated stations outside the region of greatest concentration, an unusual feature in the distribution of any species of this genus.

Gymnosporangium clavipes has been reported from southern Newfoundland, from all the provinces of Canada except Prince Edward Island, from all the states of the United States except Arizona, California, Idaho, Kansas, Minnesota, Nevada, New Mexico, North Dakota, Oregon, South Dakota and Washington. It is also reported from Mexico State in Mexico. No other species of *Gymnosporangium* is known to have a longitudinal range extending from central Mexico State to northern Alberta in Canada. An even greater range is possible on the basis of host distribution. It would be very interesting as well as of much practical value to determine the phenomena responsible for the distribution of a rust within a portion of the territory occupied by both host groups.

VII. CONTROL MEASURES APPLICABLE TO GYMNOSPORANGIUM CLAVIPES ON POMACEOUS AND ON JUNIPERUS HOSTS

Prophylactic measures to control *G. clavipes* have been largely an adaptation of those practiced for the control of the cedar-apple rust diseases caused by *G. Juniperi-virginianae*. The results obtained in control work have been essentially parallel for both of these diseases, namely, fungicidal control as practiced was found unsatisfactory, while eradication of Juniperus hosts gave excellent protection to pomaceous hosts.

Halsted (1893) reported the destruction of quince, apple, hawthorn and shadbush fruit by *G. clavipes* in New Jersey and recommended remedial measures. Concerning the disease Halsted wrote: "an enemy is beyond the fence; therefore, go out and slay him with an axe." This

was the earliest record that I found regarding the pathenogenicity and control of this rust. Bailey (1894) also recommended the destruction of red cedars as a control measure. He gave evidence to show that spraying thoroughly (with Bordeaux ?) was of considerable value. Many other authors stated that eradication of red cedars offered the most satisfactory solution to the control of this rust.

My own investigations on control measures applicable to *G. clavipes* were carried out simultaneously with those for the control of the cedar-apple rust fungus, *G. Juniperi-virginianae* (Crowell, 1934). Studies in this problem included an exploratory investigation of numerous fungicides with respect to their control value both on pomaceous hosts and on red cedars. The most promising of these fungicides were then tested on an extensive experimental scale on numerous trees under various weather conditions. The fungicides were applied to red cedars (a) to prevent germination of the teliospores, (b) to protect them from infection by aeciospores, and (c) to pomaceous hosts as a protection against basidiospore infection.

(A) Fungicidal applications on red cedars to prevent germination of teliospores

On the Lyman estate, Canton, Massachusetts, *Gymnosporangium clavipes* was in very great abundance and exploratory tests with several fungicides were made there. In table V are enumerated the sprays and dusts that were used in these tests.

TABLE V
SPRAY AND DUST MATERIALS USED IN EXPLORATORY TESTS

Bordeaux	3:3:50, 4:4:50, 6:6:50
Linco colloidal sulfur[1]	¼%, ½%, 1%, 2%, 3%
Lime-sulfur	1:30, 1:40, 1:50, 1:70
Soluble palustrex[2]	1%, 2%, 3%, 4%
" " A.	" " " "
" " B.	" " " "
" " C.	" " " "
Sunoco oil[3]	2%, 4%
50% Sunoco oil and 50% soluble palustrex	2%, 4%
50% Sunoco oil and 50% soluble palustrex B.	2%, 4%
80% Sunoco oil and 20% copper resinate	2%, 4%
80% Sunoco oil and 20% soluble palustrex	2%, 4%
Kolo base	
Kolo dust	
Pomo green	
Sulfur dust	

[1]Obtained from Linder and Co., 296 North Beacon St., Boston, Mass.
[2]Obtained from E. W. Coolidge, Jacksonville, Florida.
[3]Obtained from Sun Oil Co., Boston, Mass.

All of these spray and dust materials were first applied to potted red cedars in the greenhouse in the spring. None of them caused burning of the young foliage. In the field the sprays were applied to twig lesions as follows: (1) before the telia had emerged, (2) just after the telia had emerged, and (3) after one, two or three gelatinizations of the telia, but always when the telia were dry. Telia to which the sprays were applied were brought into the laboratory for examination; smear slides were made of the spores and examination was completed shortly after their arrival. It was not the purpose of this examination to determine the relative value of each spray, rather the purpose was to determine which ones would prevent germination of the teliospores. The most satisfactory sprays were soluble palustrex B. at 4% and Linco colloidal sulfur at 1%, 2% and 3%. In testing these sprays further it was found that this colloidal sulfur at 2% and 3% was the most constant in its reactions. Colloidal sulfur was, therefore, chosen for the experimental work that followed. It should be added, however, that colloidal sulfur at 1% greatly reduced the amount of germination; colloidal sulfur at 2% completely prevented germination of the teliospores of *G. clavipes*. Colloidal sulfur at 3%, therefore, was unnecessary.

In April 1933, many telia of *G. clavipes* were sprayed upon their first appearance with colloidal sulfur at 1% and 2%. The effect of the spray was determined by gathering several sprayed telia three days after the application and also unsprayed telia at the same time for controls, thoroughly wetting and keeping them in a moist chamber over night. When germination was abundant a spore print resulted, but when no spore print was formed a smear slide was made and the teliospores examined under the microscope. The unsprayed teliospores always germinated in abundance. Teliospores sprayed with colloidal sulfur at 1% strength germinated to some extent but few basidiospores germinated. Telia sprayed with 2% colloidal sulfur showed no germination of the teliospores.

After the rain following each spray application, telia were again gathered and immediately tested. The controls germinated in abundance. The telia sprayed with colloidal sulfur at 1% and 2% germinated to a slight extent. Some change, therefore, was called for in order to control this small amount of germination. Certain substances were used to lower the surface tension of the spray material which might aid its penetration into the telium. Spreaders were tried but with no success. Calcium casienate, a combined spreader and sticker, was next used in a series of experiments. A new lot of telia was sprayed with colloidal sulfur at the strength of 2% plus 2 pounds of calcium casienate

per hundred gallons of water. Telia tested in the laboratory showed a high percentage of germination for those that were unsprayed and no germination for those that were sprayed. In subsequent rains none of the teliospores were observed to have germinated nor did the telia at any time regain the property of gelatinizing fully, although they did gelatinize to a slight extent.

(B) Fungicidal applications on red cedars as a protection against infection by aeciospores

Fungicidal protection to red cedars against infection by aeciospores of *G. clavipes* has been demonstrated on potted red cedars in greenhouse trials. In these tests Linco colloidal sulfur at the strength of ½% or 6 pounds per 100 gallons of water only was used. Twenty-five red cedars twelve to eighteen inches high were sprayed with the fungicide. These and twenty-five unsprayed red cedars were thoroughly wetted with a strong stream from a hose the following day. They were then heavily inoculated with fresh aeciospores of *G. clavipes* and kept in a moist chamber for five days. In the spring of the second year after inoculating, each of the unsprayed plants produced an abundance of sori — a total of more than one thousand separate infections — while but a single infection was found on the sprayed plants.

In field experimentation, three applications (one each in July, August and September) were made to a group of red cedar trees near heavily infected hawthorns. Examination of the twigs the second spring after spraying showed a very marked reduction in the number of lesions produced. It was estimated after comparing the amount of infection on unsprayed red cedars in the vicinity that about 75% control was obtained.

The use of fungicidal means of protecting red cedars in practice should be guided, along with other considerations, by two important factors, namely, (1) the date of maturity of the aecia and (2) the duration of aeciospore production.

The first of these will vary with the season and with the time of blossoming of the host. In Massachusetts aecia reach maturity early in June. The second and the more variable of the two is the period of active aeciospore production. The duration of this period is dependent upon the date of maturity of the fruit of the associated pomaceous hosts. As the fruit of *Amelanchier* ripen and drop about the middle of July in Massachusetts and aeciospore production ceases at this time, protective sprays, therefore, need be applied for but a brief period. Twig infections, if present on the shadbushes, should be carefully removed, because aeciospore production will continue on them throughout the entire growing

season. On the other hand fruits of *Crataegi* and most other pomaceous hosts do not reach maturity until late fall and aeciospore production usually continues during this period.

(C) Fungicidal applications on pomaceous hosts as protection against infection by basidiospores

Fungicidal protection of pomaceous hosts from infection by *G. clavipes* has been conducted through field experiments only. Individuals of *Amelanchier oblongifolia* were sprayed with Linco colloidal sulfur at the strength of ½% or 6 pounds per 100 gallons of water after each of three rains during the early development of the flowers in the spring. Spraying was begun just before the first rain after the flower clusters began to unfold; the last application was made when about three-fourths of the petals had fallen. The protection afforded these plants was excellent. Counts of infected fruits showed that 98% of them remained free from infection, while 95% of the fruits on unsprayed plants nearby were infected. Certain other experiments with this same material on hawthorns and apples have not met with the same success. Excellent protection was afforded certain of the tested trees while practically none was obtained on others. It is believed that this irregularity can be overcome. It is not yet known just when infection occurs nor the limits of the period of susceptibility of many of the host species. A knowledge of these is necessary to satisfactory control. The value of thorough spraying cannot be over-emphasized.

Gymnosporangium clavipes is largely a fruit parasite on its pomaceous hosts, and a difficulty arises with respect to spraying while the hosts are in flower. Sprays may be applied at any time except for a few days immediately after the unfolding of the petals. It is at this time that pollination occurs. The problem of controlling the disease caused by *G. clavipes* on orchard apples has not as yet been given attention. A project to determine the limits of the period of susceptibility and modifications, if any, of the spray schedule now generally used in apple orchards is planned.

In addition to protective spray applications for the control of *G. clavipes*, other means of attack may be employed. In ornamental plantings of red or common cedars judicious pruning of infected branches and twigs is very effective. Not only will pruning remove the disease from infected trees but will afford a degree of protection to neighboring pomaceous hosts as well. The work is best done in the spring when infected parts are clearly marked by the presence of telial sori. Small twigs may be cut off below the nearest uninfected shoot, but it seems advisable that larger branches be removed well below visible lesions; in many instances this may be back to the main trunk.

The possibility of freeing infected trunks of red cedars from disease has been the subject of an, as yet, incomplete investigation. It will be recalled that the mycelium of *G. clavipes* is localized on the phellogen layer only of red cedars. Experimentation was conducted for the purpose of investigating the possibility of removal of the fungus by removing the outer bark. For this purpose a coarse wood rasp was used, and the bark, over and for about an inch around the lesion, was scraped off and painted with shellac and later with an antiseptic tree dressing. The work was done in March and no telia developed in the spring nor did the trees show visible symptoms of injury the following growing season. Only one season has passed since the undertaking and thus far the operation seems successful.

Eradication of Juniperus and of pomaceous hosts, while often limited in practice, is; nevertheless, a very effective adjunct or under certain conditions the most effective means of controlling this rust. The low growing types of junipers, such as *J. communis* and varieties and *J. horizontalis*, are frequently weed plants. In some localities in the Annapolis valley of Nova Scotia wild junipers have been eradicated for one-quarter to one-half mile around commercial orchards with the result of almost complete protection to the susceptible varieties of apples. From their observations in an apple orchard in Maine, Steinmetz and Hilborn (1934) state: "the approximate shortest distance between the infected junipers and infected apple trees is 3900 feet. The extreme distance between infected hosts is over 4500 feet." Various environmental factors, however, may influence the distance that the contagion will travel as I have already discussed in another paper (Crowell, 1934 pp. 202–209) and these should be considered in plans for eradication. As an expedient to the protection of either pomaceous or Juniperus hosts, all nearby hosts that can be dispensed with should be removed. Elaborate protective measures may be largely upset by a single weed-host plant located near valued plantings.

VIII. RECOMMENDATIONS

The problem of controlling the diseases caused by *G. clavipes* on pomaceous and on Juniperus hosts usually varies with the relative value of the infected plants and with the interest of the owner. The problem, however, merits wider attention. The moral obligation of consideration for a neighbor's earnest endeavors to improve a serious situation is too often thought of very lightly. Several practical control measures have been demonstrated. These are as follows:

1. Selection of immune or highly resistant species and varieties for planting. Attention should be given not only to avoiding hosts of *G. clavipes* but to avoiding hosts of other species of *Gymnosporangium* native in the vicinity. Host lists for all of the species of *Gymnosporangium* in eastern North America are now rapidly nearing completion. MacLachlan (1935) has shown that practically the whole of the genus *Crataegus* is more or less susceptible to attack by *G. globosum.* Many species and varieties of hawthorn are also susceptible to *G. clavipes* as shown in the present paper and to another widespread species common in this region, namely, *G. clavariaeforme.* (The presentation of results of investigations on this species is planned for an early publication.) Species and varieties of *Crataegus,* either native or foreign, cannot be planted in the vicinity of Juniperus hosts in eastern North America with expectation of their remaining entirely free from infection by one or more species of *Gymnosporangium.* In the genus *Malus,* Crowell (1934) has shown that all of the native species and varieties and one foreign species (*M. sylvestris*) can harbor and reproduce the cedar-apple rust fungus *G. Juniperi-virginianae.* The present paper and that of MacLachlan (1935) give but few additional species and varieties of *Malus* that are hosts to *G. clavipes* and *G. globosum.* All other Eurasian species and varieties do not harbor and reproduce the rusts native to this region. In the genus *Amelanchier* one species only, namely, *A. amabilis,* has proved to be highly resistant to all of the *Gymnosporangia* in this region. Other species and varieties are subject to infection by one or more species of *Gymnosporangium.*

Few hosts for the native *Gymnosporangia* were found in the genera *Pyrus* and *Sorbus* while practically all of the species and varieties tested in the genera *Aronia, Crataegomespilus, Cydonia* and *Photinia* were susceptible. Information as to the hosts in other pomaceous genera is too meagre for general recommendations at this time. For specific host lists together with the relative data of various hosts attention is directed to the present and the following publications now available. For hosts of *G. globosum,* (MacLachlan 1935). For hosts of *G. Juniperi-virginianae,* on ornamental apples (Crowell 1934); on orchard apples (Crowell 1935).

Of the telial hosts, with the exception of *Juniperus virginiana, J. horizontalis, J. scopulorum* and several of their varieties among the native species and *J. communis* and *J. Sabina* and several of their varieties among the foreign species, all other species and varieties tested (see p. 379) may be considered as desirable for plantings in this locality.

2. Planting a screen of tall non-susceptible trees about groups of alternate host plants. Groups of alternate host plants in close proximity may be effectively protected from infection by surrounding them with a screen of tall trees. Densely branching trees, as many of the conifers, are particularly effective. The corollary is also true. Groups of alternate host plants may be grown in close proximity if planted among taller non-susceptible trees. These phenomena have frequently been observed in nature. A fuller discussion is given on page 204 of an account of the cedar-apple rust disease by Crowell (1934).

3. Eradication of pomaceous or Juniperus hosts. To be most effective eradication of either pomaceous or Juniperus host plants should be complete over a radius of at least one-half mile. Even though eradication is carried out over this area, complete protection is not assured. Thus, the direction of winds during the time of spore production, continued humidity and the location of the source of inoculum are factors that may tend to offset or vary the results. A high degree of protection may be expected from eradication, however. If eradication cannot be complete, partial eradication of host plants will reduce the amount of inoculum and will therefore aid in controlling the rust. All wild or scrubby pomaceous as well as Juniperus hosts that can be dispensed with should be removed.

4. Removal of infected parts of host plants. As infections in Juniperus hosts are perennial for several years removal of diseased twigs and branches will contribute materially to control measures. Diseased twigs should be removed well below visible lesions. In the case of infected branches it may be necessary to remove them back to the main trunk. Similarly, on pomaceous hosts diseased fruits and twigs may be removed as an aid to control measures. Unless diseased parts are few in number and can be easily and thoroughly picked by hand, the undertaking is not recommended.

5. Removal of the fungus from infected trunks of red cedars. Incomplete experimentation has shown that infections on the main trunk of red cedars may be satisfactorily removed. This is done by rasping off the outer bark down to the living outer tissues, painting the wound with shellac and later with an antiseptic tree dressing. The practice is limited to trunk lesions and is not generally recommended. Removal of diseased parts or the disease from parts of Juniperus hosts is best accomplished when telia are present on infected areas to guide one in the work.

6. Protective spray applications. Protective spray applications to pomaceous plants for protection against infection by basidiospores of *G. clavipes* are of value during the early stages of development of flowers

and fruits. Linco colloidal sulfur was the only fungicide tested for this purpose. Applications at ½ % strength or 6 lbs. per 100 gallons of water plus a casein sticker are recommended. The first application should be made before the first expected rain as the cluster buds are breaking. Subsequent applications of the same strength should be made at 7–10 day intervals until most of the petals have dropped. More frequent applications may be necessary if rain is unusually heavy or prolonged, or if flowers have expanded with unusual rapidity.

Spray applications to Juniperus hosts should be confined to the period of aeciospore production on neighboring pomaceous hosts, and should be made after each two or three rains. In Massachusetts aeciospores are first liberated about June first. In the case of most species of *Amelanchier* the fruits are ripened and dropped by the middle of July. Therefore, spray applications need not be continued longer than this time, provided that *Amelanchier* species are the only hosts in the vicinity. Care should be taken, however, to remove all infected twigs from these plants for aeciospore production on them continues throughout the entire growing season. On most other hosts, aeciospores continue to be liberated during the entire growing season. Under such conditions spray applications should be continued until the end of the growing season.

The telia of *G. clavipes* are fully exposed one to two weeks before susceptible parts of pomaceous hosts are released from their buds. This affords an opportunity to attack the telia before it is possible for them to cause infection. Two spray applications of colloidal sulfur at the strength of one percent or 10–12 pounds per one hundred gallons of water are recommended. The applications should be made before buds of pomaceous hosts burst. Each application should be made just after a rain in which the telia are fully expanded and are beginning to dry. At this time they expose the greatest surface and absorb water with much avidity. It should not be expected that the fungus in the twigs and branches will be killed by this means, the telia of the present season only will be destroyed.

The relative merits of each of the foregoing means of control for *G. clavipes* will vary with individual situations. Single or a combination of methods of control may be employed. Selective planting methods will doubtless give the most permanent results but are limited in their adaptation. Methods of eradication (3, 4 and 5) may be employed where the plants are of such high value, or are few, or the rust sufficient sparse as to make hand labor practical. Spray applications are perhaps most wide in applicability since the practice of spraying is so general.

IX. SUMMARY

1. Inoculations with *Gymnosporangium clavipes* C. and P. and examinations for infection were made on approximately seven hundred species and varieties in thirteen genera of pomaceous hosts. These genera were *Amelanchier, Amelosorbus, Aronia, Chaenomeles, Crataegomespilus, Crataegus, Cydonia, Malus, Photinia, Pyrus, Sorbaronia, Sorbopyrus* and *Sorbus*. The genera *Comptonia* and *Myrica* as represented in the Arnold Arboretum were also inoculated. The results show that hosts were distributed in eleven of these genera, namely, *Amelanchier, Amelosorbus, Aronia, Chaenomeles, Crataegomespilus, Crataegus, Cydonia, Malus, Photinia, Pyrus* and *Sorbus*. Although pomaceous hosts of *G. clavipes* are found over the entire temperate region of the northern hemisphere, the fungus is confined to North America.

2. Investigations made on the period of susceptibility of flowers and fruits of certain pomaceous hosts showed that the flowers and fruits were susceptible after they were released from their buds for a brief period only. The more susceptible hosts were susceptible for a longer period than less susceptible hosts.

3. Inoculations and examinations for infection on the genus *Juniperus* in the Arnold Arboretum and accounts in the literature showed that a total of eight species and varieties were susceptible to *G. clavipes*. Hosts were found in two sections of the genus *Juniperus*. These hosts occur over essentially the same geographical range as do the pomaceous hosts.

4. The disease caused by *G. clavipes* on pomaceous hosts was found to occur most frequently on fruits, less frequently on twigs and buds and but rarely on leaves. It was most severe on fruits, twigs and buds, usually causing marked hyperplastic distortion. Infected buds were not only swollen but were forced to develop beyond the usual for the current season. On certain fruits, particularly varieties of orchard apples the disease produced was limited to small hypoplastic lesions usually at the blossom end. On leaves the disease was limited to small, usually partially necrotic, spots.

5. On its Juniperus hosts the disease was most abundant on twigs from one to five years old but was also found on leaves, branches and the main trunk. Diseased leaves were discolored and slightly swollen. They were usually killed in one or two years. The disease was perennial for several years on twigs and branches. They were usually girdled and covered with a thick, flaky or furrowed blackened bark. On the main trunk the disease lived for many years but was usually confined to elongated swollen patches covered with deeply furrowed and blackened bark.

6. The life history of the aecial phase of *G. clavipes* was essentially the same on fruits and twigs. It was slower in its development in leaves and in fruits of very resistant hosts, in fact in the latter it was often aborted. In forced buds the mycelium was essentially systemic and developed spermogonia, rarely aecia, progressively as the buds elongated.

7. The mycelium of the telial phase of *G. clavipes* was confined to the epidermis of leaves and to the phellogen of twigs, branches and the main trunk of its Juniperus hosts. It remained in leaves for but one, occasionally for two years. It was perennial for several years in twigs, branches and the main trunk. Telia were produced annually on infected organs.

8. Several means have been demonstrated for the control of *G. clavipes* on pomaceous and on Juniperus hosts. Especial attention has been given to finding satisfactory fungicides and formulating practical spray programs. Of the fungicides tested Linco colloidal sulfur gave very promising results. It was the only one used in field experimentation.

9. Recommendations with respect to the control of this rust have been discussed under the headings of: selective plantings, eradication of hosts, removing infected parts from pomaceous and Juniperus hosts, removing infections from trunks of red cedars and spray applications on pomaceous and Juniperus hosts.

BIBLIOGRAPHY

ADAMS, J. F. (1916). Internal Uredineae. (Mycologia, **8**: 181–182.)
——— (1919). Rusts on conifers in Pennsylvania — I. (Pennsylvania Agric. Exper. Sta. Bull. **160**: 1–30.)
——— (1921). Observations on the infection of Crataegus by Gymnosporangium. (Mycologia, **13**: 45–49.)
ARTHUR, J. C. (1901). Generic nomenclature of cedar apples. (Proc. Indiana Acad. Sci. **1900**: 131–136.)
——— (1909). Cultures of Uredineae in 1908. (Mycologia, **1**: 225–256.)
——— (1929). Plant rusts. (John Wiley and Sons, New York, 446pp.)
——— (1934). Manual of the rusts in United States and Canada (Purdue Research Foundation, Lafayette, Indiana, 438pp.)
BAILEY, L. H. (1894). Rust in The Quince in western New York. (Cornell Univ. Agric. Exper. Sta. Bull. **80**: 625–627.)
BEACH, S. A. (1905). The apples of New York. (New York Agric. Exper. Sta. Rep. 1903, Vols. I and II.)
COOKE, M. C. and C. H. PECK (1871). Note on Podisoma. (Jour. Quekett Micr. Club, **2**: 255–268.)
COONS, G. H. (1912). Some investigations of the cedar rust fungus, Gymnosporangium Juniperi-virginianae Schw. (Ann. Rep. Nebraska Agric. Exper. Sta. **25**: 217–245.)

CRABILL, C. H. (1913). Production of secondary sporidia by Gymnosporangium. (Phytopath. **3**: 282–284.)
CROWELL, I. H. (1934). The hosts, life history and control of the cedar-apple rust fungus Gymnosporangium Juniperi-virginianae Schw. (Jour. Arnold Arb. **15**: 163–232.)
——— (1935). Compilation of reports on the relative susceptibility of orchard varieties of apples to the cedar-apple rust disease. (Proc. Amer. Soc. Hort. Sci. for 1934. **32**: 261–272.)
——— (1935). Unusual developments of cedar rusts on pomaceous hosts in 1935. (Plant Disease Reporter, **19**: 197–198.)
DODGE, B. O. (1918). Studies in the genus Gymnosporangium — I. Notes on the distribution of the mycelium, buffer cells and the germination of the aecidiospores. (Brooklyn Bot. Gard. Mem. **1**: 128–140.)
——— (1918). Studies in the genus Gymnosporangium — II. Report on cultures made in 1915 and 1916. (Bull. Torrey Bot. Club, **45**: 287–300.)
——— (1918). Studies in the genus Gymnosporangium — III. The origin of the teleutospore. (Mycologia, **10**: 182–193.)
——— (1922). Studies in the genus Gymnosporangium — IV. Distribution of the mycelium and the subcuticular origin of the telium in G. clavipes. (Amer. Jour. Bot. **9**: 354–365.)
——— (1924). Aecidiospore discharge as related to the character of the spore wall. (Jour. Agric. Res. **27**: 749–756.)
——— (1924). Expulsion of aecidiospores by the May apple-rust. Puccinia podophylli Schw. (Jour. Agric. Res. **28**: 923–926.)
——— (1931). Studies in the genus Gymnosporangium — V. A destructive red cedar rust disease. (Jour. New York Bot. Gard. **32**: 101–108.)
——— (1933). The orange rust of hawthorn and quince invades the trunk of red cedar. (Jour. New York Bot. Gard. **34**: 233–237.)
FARLOW, W. G. (1880). The Gymnosporangia or cedar-apples of the United States. (Anniversary Memoirs Boston Soc. Nat. Hist. [Sci. Papers, 4], 2pl.)
——— (1881). Notes on Gymnosporangia. (Bull. Torrey Bot. Club, **8**: 85–87.)
——— (1885). Notes on some species of Gymnosporangium and Chrysomyxa of the United States. (Proc. Amer. Acad. Arts and Sci. **20**: 311–323.)
FUKUSHI, T. (1925). Studies on the apple rust caused by Gymnosporangium Yamadae Miyabe. (Jour. Col. Agric. Hokkaido Imp. Univ. **15**: 269–307.)
HOCKEY, J. F. (1926). Report of the Dominion field laboratory of plant pathology, Kentville, Nova Scotia. (Rep. Dominion Botanist 1925, **38**.)
KERN, F. D. (1910). The morphology of the peridial cells of the Roesteliae. (Bot. Gaz. **49**: 445–452.)
——— (1911). A biologic and taxonomic study of the genus Gymnosporangium. (Bull. New York Bot. Gard. **7**: 391–483.)
MACLACHLAN, J. D. (1935). The hosts of Gymnosporangium globosum Farl. and their relative susceptibility. (Jour. Arnold Arb. **16**: 98–142.)
MILLER, P. R. (1932). The pathogenicity of three red cedar rusts that occur on apple. (Phytopath. **22**: 723–740.)
MILLS, W. D. (1929). Cedar rusts, Gymnosporangium Juniperi-virginianae, G. globosum and G. germinale. (Plant Disease Reporter, Supp. **70**: 188.)

PADDOCK, W. (1902). Quince rust. (Plant diseases of 1901. Colorado Agric. Exper. Sta. Bull. **69**: 18–20.)
PALMER, E. J. (1925). Synopsis of North American Crataegi. (Jour. Arnold Arb. **6**: 5–128.)
PAMMEL, L. H. (1905). Cedar apple fungi and apple rust in Iowa. (Iowa Agric. Exper. Sta. Bull. **84**: 1–36.)
PECK, C. H. (1873). Report of the Botanist. (Ann. Rep. New York State Mus. Nat. Hist. **25**[1871]: 57–123.)
RAGAN, W. H. (1905). Nomenclature of the apple. (U. S. Dept. Agric. Bull. **56**, issued 1926, 1–396.)
REHDER, A. (1927). Manual of cultivated trees and shrubs. (Macmillan and Co., New York, 930pp.)
SCHWEINITZ, L. D. (1832). Synopsis fungorum in America Boreali media degentium. (Trans. Amer. Phil. Soc. II. **4**: 141–316.)
STEINMETZ, F. H. and M. T. HILBORN (1934). Observations on Gymnosporangium germinale. (Phytopath. **24**: 833–834.)
STONE, G. E. and R. E. SMITH (1898). The quince rust. (Rep. Massachusetts Agric. Exper. Sta. **10**: 61–63.)
STONE, R. E. (1909). Studies of Gymnosporangium in southern Alabama. (Torreya, **9**: 114–117.)
SYDOW, P. and H. (1915). Monographia Uredinearum. III.
THAXTER, R. (1887). On certain cultures of Gymnosporangium with notes on their Roesteliae. (Proc. Amer. Acad. Arts and Sci. **22**: 259–269.)
——— (1889). Notes on cultures of Gymnosporangium made in 1887 and 1888. (Bot. Gaz. **14**: 163–172.)
——— (1891). The Connecticut species of Gymnosporangium (cedar-apples). (Connecticut Agric. Exper. Sta. Bull. **107**: 1–6.)
THOMAS, H. E. (1933). The quince rust disease caused by Gymnosporangium germinale. (Phytopath. **23**: 546–553.)
——— and W. D. MILLS (1929). Three rust diseases of the apple. (Cornell Agric. Exper. Sta. Mem. **123**: 1–21.)
——— ——— (1930). Rust diseases of the apple. (Plant Disease Reporter, **14**: 214–215.)
TUBEUF, K. VON (1906). Uberwinterung des Birnenrostes auf dem Birnbaum. (Nat. Zeits. Land Forstw. **4**: 150–152.)
——— (1907). Perennieren des Aecidien mycels vom Birnenrostpilz. (Nat. Zeits. Land Forstw. **5**: 217–219.)
WEIMER, J. L. (1917). Three cedar rust fungi, their life histories and diseases they produce. (Cornell Agric. Exper. Sta. Bull. **390**: 507–549.)

EXPLANATION OF THE PLATES

PLATE 155[1]

Fig. 1. Progressive stages are shown in the exposure and rupturing of aecial fructifications of *Gymnosporangium clavipes* on an orchard apple.
Fig. 2. The dark colored lesion was caused by an imperfect fungus. Aecial fructifications of *G. clavipes* are shown on the upper portion of the lesion.
Fig. 3. Infected twig and fruit of *Cydonia oblonga*, the quince.

[1]Figures 1, 2 and 3 were obtained through the courtesy of Mr. K. A. Harrison of the Dominion Experimental Farms, Kentville, N. S.

Fig. 4. This shoot of *Amelanchier oblongifolia* was inoculated with teliospores of *G. clavipes.* Infection occurred, however, on the fruits and pedicels only.
Fig. 5. Fruits of *Crataegus mollis* infected with *G. clavipes.*
Fig. 6. Fruits of *Malus floribunda* infected with *G. clavipes.*

PLATE 156

Fig. 1. Twig and thorns of *Crataegus* sp. infected with *G. clavipes.*
Fig. 2. Forced growth of infected buds of *Crataegus mollis.* The diseased buds on the twigs of this species have enlarged greatly. Compare with the normal buds on the twig shown on the extreme right.
Fig. 3. Another manifestation of the forced growth of infected buds on *Crataegus* sp. On this species the buds and stems have enlarged but little while the leaves, though small, have taken on features of normal maturity.
Fig. 4. Another manifestation of the forced growth of infected buds on *Crataegus* sp. On this host the buds have swollen considerably and the young stems have elongated but the leaves have remained quite stunted in their growth.
Fig. 5. Infected shoot of *Crataegus Phaenopyrum.* This type of symptom was also found on the English hawthorn, *C. Oxyacantha.*
Fig. 6. A globose gall-like swelling of an infected twig of *C. Oxyacantha.*
Fig. 7. Spermogonium of *G. clavipes.* Note its deep, sunken location and rotund form.

PLATE 157

Fig. 1. Normal aeciospore chain of *G. clavipes.* Note the regular occurrence of aeciospores and intercalary cells.
Fig. 2. Abnormal aeciospore chain. The aeciospores are irregular in shape as well as in their arrangement with respect to the intercalary cells.
Fig. 3. Outline drawings of aeciospores of *G. clavipes.*
Fig. 4. Camera lucida drawings of germinating aeciospores of *G. clavipes.*
Fig. 5. Face and side views of peridial cells of *G. clavipes.*
Fig. 6. Outline drawings of peridial cells of *G. clavipes.*
Fig. 7. Camera lucida drawings of haustoria of *G. clavipes* as seen in the cells of fruits and twigs of various pomaceous hosts. All forms shown may be found in the same organ of any specific host.

PLATE 158

Fully gelatinized telia of *G. clavipes* on branches of red cedar. The bright red sori are very conspicuous during spring rains.

PLATE 159

Fig. 1. Trunk lesion caused by *G. clavipes* on red cedar. Lesions are typically oval in outline and the bark over them is darker in color than normal bark. Note the former location of a branch near the center of the lesion.
Fig. 2. Several trunk infections on a red cedar tree. Note that the trunk lesions are found in connection with lateral branches; many of these have died and been removed.
Fig. 3. Telia of *G. clavipes* in their last stages of gelatinization. At this time they are almost shapeless masses.

Fig. 4. A slight swelling of the twig and a darker color of the bark are typical of the lesions on twigs of red cedars. These photographs were taken in mid-winter.
Fig. 5. Cross section of a telium of *G. clavipes* on *J. virginiana*. Note the pulvinate form of the sorus.

PLATE 160

Fig. 1. Shows diagrammatically the location of the telia and the course of extension of the mycelium of *G. clavipes* over the phellogen of its host. This is a camera lucida drawing.
Fig. 2. The mycelium of *G. clavipes* in an early stage of extension over the new phellogen that has recently connected with the existing one. Note that the mycelium is found on the phellogen only of its host.
Fig. 3. Formation of the telial sorus. Buffer cells are in various stages of development. It will be observed here also that the mycelium does not penetrate beneath the phellogen.
Fig. 4. Early stages in the development of teliospores. The teliospore initials are elongating into the buffer cells.
Fig. 5. Stages in the maturation of teliospores. These stages are similar to those for the maturation of teliospores of *G. Juniperi-virginianae*.
Fig. 6. Haustoria in the phellogen cells of red cedar. They stand out clearly in prepared sections. Two and three haustoria are commonly found in a single host cell.

LABORATORY OF PLANT PATHOLOGY,
ARNOLD ARBORETUM, HARVARD UNIVERSITY.